How and where to restore habitat on farmland to increase the abundance and diversity of moths

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by

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Abstract

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Modern agriculture has severely impacted the variety of life on earth. Agricultural expansion has cleared >50% of natural habitats on agriculturally usable land, while agricultural intensification has reduced the abundance and diversity of wildlife in farmed areas. Agri-environment schemes (AESs) offer opportunities to restore habitats for wildlife in farmed landscapes across Europe and elsewhere. This could help to (1) reverse declines in species of conservation concern and (2) provide "ecosystem services", such as pollination, which contribute to human wellbeing.

AES interventions have led to increases in the abundance and diversity of wildlife. However, despite the scale of public investment in AESs, the size and significance of those increases are often unclear. Furthermore, the outcomes of AES interventions vary depending on features of the surrounding landscape, especially semi-natural habitat. Research to date has directed the allocation of AES interventions in a broad sense, for example towards landscapes with <20% coverage of semi-natural habitat. Still, there is a lack of specific advice about how and where to restore habitat on farmland to maximise benefits for priority insect species.

I present two field studies of the abundance and species richness of night-flying Lepidoptera (moths) in the UK, aiming to develop advice for land managers implementing AESs. Focussing on moths in three distinct habitat specialism groups, I looked at how the benefits of two types of AES interventions were affected by the coverage of semi-natural calcareous grassland (CG) nearby.

In the first field study I investigated the benefits of AES interventions that create wide grass margins on the edges of arable fields. I found that grass margins significantly increased the abundance of grassland generalist moths. Furthermore, grass margins benefitted CG-associated moths if there were large areas of CG habitat nearby. Therefore, spatial targeting of AES interventions towards semi-natural habitat has the potential to improve outcomes for biodiversity.

In the second field study I investigated the benefits of AES interventions that restore arable fields to species-rich grassland. Restored grassland fields were similar to semi-natural CG in terms of moth abundance and species richness. Furthermore, CG moths were more abundant on restored grassland where CG indicator wildflowers were established. Grassland restoration is a particularly successful AES intervention, especially if the plant community is enhanced to support priority insect species.

Finally, I present the first individual-based model to test how the benefits of AES interventions depend on distance from source populations on semi-natural habitat. By simulating larval and adult life-stages of hypothetical insect species, my model provided a set of mechanisms that help to explain my empirical field observations.

Ultimately, this thesis presents two of the most robust field studies on the interaction between AES interventions and the landscape context. By interpreting these field studies in light of a supporting model, I produce clear advice for land managers interested in the conservation of moths and the other species with which they coexist.

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Contents

Abbreviations:		
	AES	Agri-environment scheme
	CG	Calcareous grassland
	SNH	Semi-natural habitat
	HLS	Higher Level Stewardship
	SSSI	Site of Special Scientific Interest

Chapter 1: Where are agri-environment schemes best placed to increase biodiversity and ecosystem services? A literature review

1.1.Preface

This chapter provides an overview of agri-environment schemes (AESs), which subsidise wildlife-friendly management on farmland, as well as how their effects are dependent on features of the surrounding landscape. Following a brief introduction to human-induced pressures on the variety of life on earth (1.2. Background), I define AESs and outline their key objectives (1.3. Definition and purpose of agri-environment schemes). I then summarise studies that have evaluated the effects of AESs on the abundance or diversity of wildlife (1.4. Do agri-environment schemes enhance biodiversity?), and highlight the key factors affecting the outcomes of AES interventions (1.5. What are the factors affecting the biodiversity benefits of agri-environment schemes?). Of those key factors I focus on the landscape context, and cover the theory of how and why this affects the outcome of AES interventions (1.6. How does landscape context affect the biodiversity benefits of agri-environment schemes?). I outline two key perspectives about the optimal placement of AES interventions to increase the abundance and diversity of wildlife (1.7. Spatial targeting of agri-environment schemes: Two key perspectives), and explore whether each is supported by relevant empirical evidence (1.8. Evidence of the effects of landscape context on the biodiversity benefits of AES interventions). Finally, I synthesise advice about where to put AES interventions using information currently available on the subject (1.9. Where should agri-environment schemes be placed to achieve their ultimate objectives?), and explore how future research might help AESs to achieve their goals in a cost-effective way (1.10. Toward optimal placement of agri-environment schemes). Importantly, this chapter provides definitions and background information that will aid interpretation of Chapters 2 to 4.

1.2.Background

The size of the human population has increased rapidly over the last five decades, and so has per capita demand for food (Tilman *et al.* 2011). These increases are likely to continue, and over time larger areas of land are being farmed using greater amounts of water, fertilizers and pesticides per unit area (Tilman *et al.* 2001a). This expansion and intensification of agriculture increases the supply and thus decreases the price of food, but also contributes greatly to greenhouse-gas emissions (Lal 2008), water and air pollution (Erisman *et al.* 2008) and soil erosion and degradation (Pimentel *et al.* 1995). At the same time, modern agriculture has led to massive reductions in the variety of life on earth (i.e. biodiversity, CoP 1992) and may threaten more species with extinction than any other sector (Green *et al.* 2005; Balmford, Green & Phalan 2012). Biodiversity is thought to underpin ecosystem functions that benefit people, for example primary production and soil formation (Tilman *et al.* 2001b; Cardinale *et al.* 2012). However, modern agriculture often bypasses these functions using chemical energy derived from unsustainable sources. For example, non-renewable fossil fuels are used to power the manufacture, transport and spread nitrogen fertilizer (Jensen & Hauggaard-Nielsen 2003; Swift, Izac & van Noordwijk 2004). Overall, management interventions that enhance biodiversity are considered important not only to conserve rare or threatened species, but to increase the wide ranging and sustainable benefits that ecosystems can provide for people (Bommarco, Kleijn & Potts 2013).

1.3.Definition and purpose of agri-environment schemes

Agri-environment schemes (AESs) can be defined as subsidies for interventions that aim to enhance biodiversity on farmland, often by restricting farming intensity (Kleijn *et al.* 2011). AES interventions can take a variety of forms, with practices ranging from organic farming (Rundlöf & Smith 2006) to reduced grazing intensity on grassland (Kruess & Tscharntke 2002a; b) to maintaining wide grass margins on arable fields (Merckx *et al.* 2009a) to converting entire arable fields to species-rich grassland (Critchley, Burke & Stevens 2003). Given that AES interventions are usually defined based on the immediate aim to enhance biodiversity, it is unsurprising that they are so

varied; biodiversity is multi-faceted, and can be enhanced in countless ways. As such, it is helpful to consider the ultimate objectives of AESs, which can be usefully divided as follows: (1) the enhancement of threatened aspects of biodiversity that have intrinsic value or are of conservation concern and (2) the enhancement of functional aspects of biodiversity to aid sustainable delivery of a wide range of ecosystem services (i.e the benefits that ecosystems provide for human wellbeing, MEA 2005; Kleijn *et al.* 2011; Ekroos *et al.* 2014).

The first objective, to use AES interventions to benefit species threatened with decline or extinction, reflects international targets that have been set with regard to biodiversity. For example, Target 12 of the Aichi biodiversity targets requests that "By 2020 the extinction of known threatened species has been prevented and their conservation status, particularly of those most in decline, has been improved and sustained" (Secretariat of the CBD 2017). A focus on rare and threatened species has been justified based on the permanence of extinction – as Pimm *et al.* (1995) note: "Ingenuity can replace a whale-oil lamp with an electric light bulb, but not the whales we may hunt to extinction." It has also been argued that species have an intrinsic right to exist, and that humans have a responsibility to restore abused habitats to wilderness and reintroduce extirpated animals (Soulé & Noss 1998). Unprecedented rates of extinction following human activity form the backdrop for the conservation of threatened species. Recent extinction rates are 100 to 1000 times greater than pre-human estimates (Pimm *et al.* 2014), in what is considered by some to be the sixth mass extinction event in a new epoch termed the "Anthropocene" (Ceballos, Ehrlich & Dirzo 2017).

The second objective, to use AES interventions to provide ecosystem services such as pollination, flood prevention and recreation, also reflects international targets on biodiversity. Target 14 of the Aichi biodiversity targets requests that "By 2020, ecosystems that provide essential services […] and contribute to health, livelihoods and well-being, are restored and safeguarded" (Secretariat of the CBD 2017). A focus on ecosystem services has been justified based on the fact that non-food benefits of ecosystems are highly undervalued, which has potentially detrimental consequences for

human welfare (Costanza *et al.* 1997; Power 2010). Furthermore, current levels of agricultural expansion and intensification may undermine food production in future through negative externalities caused by over-extraction of water, soil degradation and environmental pollution (Foley *et al.* 2005; Godfray *et al.* 2010). Restoring ecosystem services on farmland has potential to maintain or increase yields in ways that are more sustainable than increasing agro-chemical inputs, especially in light of increasing energy costs and pesticide resistance (Bommarco, Kleijn & Potts 2013).

Any discussion of the optimisation of AES interventions should heed recent research showing that objectives to conserve threatened species and to restore ecosystem services do not always integrate well. While some AES interventions might contribute to achieving both objectives, conservation of threatened species won't necessarily correspond to increased ecosystem services – and vice versa. Evidence is accumulating that the bulk of ecosystem services, particularly pollination, is provided by a subset of common species and not by species that are rare or threatened (Kleijn *et al.* 2015; Winfree *et al.* 2015). Furthermore, while improved population demographics may be necessary to conserve threatened species, a change in the distribution of individuals may be adequate to increase ecosystem services (Kleijn *et al.* 2011). A recent meta-analysis suggests that interventions which increase biodiversity in general will tend to also restore ecosystem services (Benayas *et al.* 2009). However, it has been argued that more utilitarian interventions, with the sole aim of restoring ecosystem services, are less likely to correspond to increases in wider biodiversity (Swift, Izac & van Noordwijk 2004; Macfadyen *et al.* 2012). Given these uncertainties, it is desirable to evaluate AES interventions based on their effects on biodiversity in general, but also those aspects of biodiversity which are threatened or which are key for provision of ecosystem services. Despite this, much of the existing literature on AES interventions uses general "biodiversity" measures as proxies for the state of both ecosystem services and threatened species.

The assertion made here and elsewhere (Kleijn *et al.* 2011; Ekroos *et al.* 2014), that ultimate objectives of AESs are (1) to benefit species of conservation concern and

(2) to increase ecosystem services, largely aligns with statements in official AES documentation. For example the Entry Level Stewardship, an AES open to all farmers in England from 2005-2014, has environmental objectives to manage habitats for declining bats and dormice, but also to manage land for cleaner water and healthier soil (Natural England 2012). Nonetheless, some AES interventions are clearly designed for other objectives, for example to preserve the character of the farmed landscape or maintain anthropogenic features of historic or cultural importance. Such interventions and objectives are not considered in this review, and it is generally unclear whether they contribute to biodiversity conservation or ecosystem services.

In this review I focus on changes in the abundance and diversity of wildlife resulting from AES interventions, although biodiversity could also be enhanced according to a variety of other measures. For example, AESs can have "protection effects" by preventing declines in biodiversity due to agricultural abandonment or intensification (Kleijn *et al.* 2011). However, protection effects can only be quantified using longitudinal datasets which are rarely available (but see Taylor & Morecroft 2009), so I do not consider them explicitly here. Furthermore, AESs could help ecosystems withstand or recover rapidly from disturbances such as extreme weather events (i.e. increase ecological resilience), for example by increasing habitat connectivity (Lawton *et al.* 2010). While resilience is increasingly relevant for biodiversity conservation under climate change (Morecroft *et al.* 2012) it is not considered here because it is difficult to define and measure, and the effects of AESs on resilience are poorly understood.

1.4.Do agri-environment schemes enhance biodiversity?

Many studies have looked at the effects of AES interventions on the abundance and/or diversity of a variety of species groups across Europe, particularly birds, bees, butterflies, moths, hoverflies and plants (e.g. Kleijn *et al.* 2001; Rundlöf, Edlund & Smith 2010; Fuentes-Montemayor, Goulson & Park 2011; Pywell *et al.* 2012). However, early reviews were unable to confirm the benefits of AESs for biodiversity because empirical studies had not collected adequate control data (Kleijn & Sutherland 2003). To

understand benefits of AESs it is at least necessary to determine biodiversity on paired sites with and without interventions. Nonetheless, many recent meta-analyses have revealed positive overall effects of a broad suite of AESs on biodiversity (Batáry *et al.* 2011, 2015; Scheper *et al.* 2013; Gonthier *et al.* 2014; Tuck *et al.* 2014). As such, it seems apt to conclude that AESs have had moderately positive effects on biodiversity in Europe, particularly at local scales, with some exceptions (e.g. Kleijn *et al.* 2001).

While changes in local abundance and diversity of species form the focus of most studies of AES interventions, these cannot always reliably indicate change in critical population parameters such as birth rates and carrying capacities. For example, AES interventions could simply affect the movement of individuals, causing them to congregate nearby, without actually increasing reproduction. Even so, increases in local abundance and species richness on AES interventions might give a conservative impression of increases in reproductive rates. For example spill-over effects could occur, whereby individuals disperse away from their natal habitat into more hostile environments. These spill-over effects might lead to underestimation of the suitability of high-quality AES sites and overestimation of the suitability of low-quality sites (Kleijn *et al.* 2011). While it is becoming clear that AES interventions lead to increases in the abundance and diversity of species, it is often unclear whether they help meet targets to halt biodiversity declines; few studies have explicitly linked AES interventions to national trends in biodiversity (Kleijn *et al.* 2011). However, Vickery *et al.* (2004) have identified the resources provided by AESs in England, highlighting their potential to reverse declines in farmland birds. Accordingly, a recent study by Walker *et al.* (2018) found that population trends of priority farmland bird species tend to be more positive on farmland managed under Higher Level Stewardship (a top-tier AES in England, NE 2013) than elsewhere.

1.5. What are the factors affecting the biodiversity benefits of agri-environment schemes?

The extent to which AESs benefit biodiversity has been contested (Sutherland 2002), which is unsurprising given the breadth of different management techniques involved. It

346 is quite universally agreed that AES benefits depend on the management intervention
347 and species group in question, as well as the surrounding landscape context
348 (Whittingham 2011; Kleijn *et al.* 2011). Effects of the landscape context will form the
349 primary focus of this review, but it is first necessary to outline other potentially
350 confounding sources of variation in the effects of AESs.

351 Some types of AES intervention enhance aspects of biodiversity more than
352 others. For example, Fuentes-Montemayor *et al.* (2011) found that AES management to
353 do with grassland or field margins increased the abundance of moths on farmland, while
354 management to do with hedgerows did not. On the other hand, Batáry *et al.* (2015)
355 found that AESs which apply to non-productive areas of a farm, or which take farmland
356 out of production, have a greater positive effect on species richness than AESs which
357 apply to productive areas of a farm (e.g. organic farming). Notably, the results of AES
358 interventions may differ depending on whether management introduces target species, or
359 provides key resources that were not present beforehand (i.e. the 'ecological contrast'
360 created by management, Scheper *et al.* 2013). For example, uncropped margins sown
361 with pollen- and nectar-rich plants provide a high concentration of forage flowers for
362 pollinating insects (Carvell *et al.* 2007). It results that AES interventions that are
363 evidence-based can have increased benefits for biodiversity compared with those that are
364 more generalized. For example, Pywell *et al.* (2012) found that arable field margins
365 sown with pollen- and nectar-rich plants led to greater increases in the biodiversity of
366 bees than margins sown only with grasses. Nonetheless, there are examples where even
367 non-tailored AES interventions have increased the abundance of rare and threatened
368 species, such as the moth *Polia bombycina* (Hufnagel; Merckx *et al.* 2010b).

369 The effects of AES interventions also clearly vary between species groups,
370 corresponding to differences in species' life-history characteristics. In the study of
371 Pywell *et al.* (2012), generalised AES interventions were associated with moderate
372 increases in species richness of common bees, but not rare bees. Similarly, Alison *et al.*
373 (2016) found that grass margins clearly increased the abundance of grassland generalist
374 moths, while increases in calcareous grassland specialist moths were less obvious.

Mobility has been shown to be an important determinant of species' responses to AES interventions: moth species which travel shorter distances in agricultural landscapes have been shown to respond more positively to wide grass margins (Merckx *et al.* 2009a). The same pattern has been suggested to occur more broadly, based on evidence that mobile vertebrates respond less clearly than plants and insects to wildlife-friendly farming at local scales (Gonthier *et al.* 2014). However, species mobility could simply affect the detectability of AES benefits at local scales. Spill-over effects (defined above) are likely to be stronger for more mobile species, so that differences in abundance between AES interventions and control sites are less clear.

Clearly AES interventions can enhance biodiversity at a variety of spatial and temporal scales. Different species groups respond to AES interventions at different, and often multiple, spatial scales and this may be linked to their mobility (Gabriel *et al.* 2010). Many AES interventions take place at the field scale and below, despite the fact that many species, including some farmland birds in Europe, depend on resources at regional scales and above (Whittingham 2007, 2011; Gregory *et al.* 2008; Kleijn *et al.* 2011). To address this, researchers argue that AES interventions should take the form of large-scale habitat restoration (Sutherland 2002) or be coordinated across multiple farm units (Merckx *et al.* 2009b; McKenzie *et al.* 2013). AES interventions may also fail to provide resources on appropriate temporal scales. For example, winter food resources for birds may not be provided late into the winter when they are most needed (Siriwardena 2010), while some uncultivated field margins do not provide pollen and nectar for insects throughout the season (Carvell *et al.* 2007). Nonetheless, even where AES interventions such as organic farming cause gains to species-richness at the field scale, this may not lead to gains at the scale of the entire farm (Schneider *et al.* 2014).

1.6. How does landscape context affect the biodiversity benefits of agri-environment schemes?

Recent research has shown that landscape context is a major factor determining the extent of biodiversity benefits provided by AES interventions (Heard *et al.* 2007; Batáry *et al.* 2011; Scheper *et al.* 2013; Alison *et al.* 2016). In some cases abiotic elements of

the landscape, including geology, hydrology, climate and soil chemistry, could mediate the benefits of AES interventions. For example, Fagan *et al.* (2008) found that high soil phosphorus was detrimental to restoration of calcareous grassland under AESs in the UK. However, the biotic element of the landscape context is also critical in determining species' occupancy of habitats at local scales. This is demonstrated globally by the dependence of local species richness on the pool of species present at regional scales (Gaston 2000).

One example of how landscape-level biodiversity mediates the benefits of AES interventions can be explained based on simple meta-population dynamics: Suppose multiple species exist in a landscape comprising suitable habitat patches surrounded by a hostile matrix. Those species are dispersal-limited and do not interact with one-another, while habitat patches vary in size. Larger occupied patches can support larger populations, so they produce more emigrants and play a critical role in the colonisation and re-colonisation of small habitat patches nearby (Hanski 1994). It follows from this basic scenario that a habitat patch will tend to contain larger populations of a greater number of species if it is closer to other large habitat patches (Diamond 1975). Thus, if AES interventions create new habitat patches it could be proposed that they would be most beneficially located as close as possible to source populations. For example, Kohler *et al.* (2008) found that semi-natural grasslands in the Netherlands acted as source populations for forbs and pollinating insects, and went on to recommend preferential implementation of AESs in very close proximity to that habitat.

However, biodiversity benefits are not necessarily maximised when AES interventions are placed adjacent to source populations. Benefits are generally quantified by comparing biodiversity between AES interventions and nearby control sites (Kleijn & Sutherland 2003). Thus, to reason that AES interventions with the highest biodiversity are most beneficial is to assume that biodiversity on control sites is constant throughout the landscape. This is not true in real situations; even control sites managed as cropland, which may be considered non-habitat for most species, receive spill-over of individuals from natural and semi-natural habitats nearby (Tscharntke, Rand & Bianchi 2005). In

this regard some control sites might be "sink habitat" where reproduction does not balance local mortality (Pulliam 1998). To further complicate matters, control sites could have some reproductive value (i.e. they could be "low-quality" habitat), but appear to be sink habitat due to spill-over from high-quality habitat (Watkinson & Sutherland 1995). Overall, source populations in the landscape affect the benefits of AES interventions by (1) allowing AES interventions to be colonised and (2) causing spill-over into areas without AES interventions.

Furthermore, many species move through and interact with the landscape in complex ways (Tscharntke & Brandl 2004). For example, some species use separate habitats for nesting and foraging, in which case both habitat types would affect the distribution of individuals throughout the landscape (Westphal, Steffan-Dewenter & Tscharntke 2003). Furthermore, some species change their dispersal behaviour when they encounter different land-use types (Schultz & Crone 2001; Ovaskainen *et al.* 2008), or use boundary features such as hedgerows to guide their movement (Dover & Settele 2009). Some species even exhibit long-range perception and memory of landscape features (Conradt *et al.* 2000). All of the above behaviours could have important implications for how the landscape context mediates the benefits of AES interventions. For example, species with long-range perception and memory of foraging resources might have higher densities in isolated AES interventions, where individuals cannot detect alternative resources nearby (Heard *et al.* 2007). On the other hand, AES interventions could provide sensory cues which cause species to prefer them to the habitats that would actually confer higher fitness, making them 'ecological traps' (Battin 2004).

1.7.Spatial targeting of agri-environment schemes: Two key perspectives

Landscapes across Europe are dominated by intensive farmland with high mechanical and agro-chemical inputs, and scarcely any areas can be considered "natural" (Fisher *et al.* 2010). However, some land is managed at very low intensity, for example through forestry or grazing, and may comprise semi-natural habitat. These areas are often contained in protected areas, which tend to support higher abundances of most species

than elsewhere (Gillingham *et al.* 2014). It has recently become clear that the effects of AES interventions may differ greatly depending on the characteristics of the landscape in which they are situated. As a result, advice is emerging about how AES interventions might be spatially targeted to maximise the benefits provided to biodiversity (Perkins *et al.* 2011; Batáry *et al.* 2011; Scheper *et al.* 2013).

Understanding of how AES benefits depend on the landscape context has been advanced from two key perspectives, based on two proposed relationships which are not mutually exclusive (also outlined in Kleijn *et al.* 2011; Ekroos *et al.* 2014). The first considers the shape of the relationship between biodiversity and land-use intensity (Fig. 1, Kleijn & Sutherland 2003). The second considers the shape of the relationship between the biodiversity benefits of AES interventions and the complexity of the surrounding landscape, which is usually represented as the proportion of semi-natural habitat (Fig. 2, Tscharntke *et al.* 2005). These two perspectives have dominated the debate on the interaction between AESs and the landscape (Ekroos *et al.* 2014) although other many other aspects of the landscape context could have important effects. For example the benefits of AES interventions could vary with the coverage of arable land, or the abundance of floral resources nearby (Heard *et al.* 2007; Carvell *et al.* 2011).

The first perspective, called the "land-use-moderated conservation effectiveness hypothesis", emerged based on the observation that extensively-managed farmland has high habitat heterogeneity and biodiversity (Benton, Vickery & Wilson 2003; Kleijn & Sutherland 2003; Kleijn *et al.* 2011). As land-use intensity increases, it is proposed that biodiversity declines exponentially (Fig. 1). It results that a given reduction in land-use intensity corresponds to a greater increase in biodiversity in more extensively farmed areas (Kleijn & Sutherland 2003). It also results that avoiding increases in land-use intensity is most critical in extensively farmed areas due to increased "protection effects" (described in Fig. 1). This biodiversity-land-use relationship is comparable to density-yield functions (Green *et al.* 2005), which have been used to compare land-use strategies based on wildlife friendly farming to strategies based on "land sparing": intensive farming outside of strict conservation zones (Phalan *et al.* 2011). However, the

biodiversity-intensity relationship may be more directly relevant to AES interventions than the density-yield relationship. This is because reduction in agricultural intensity, but not reduction in yield, is considered to be a key mechanism by which AES interventions affect biodiversity (Kleijn *et al.* 2011).

The second perspective has been called the "intermediate landscape-complexity hypothesis" (Tscharntke *et al.* 2012), and it explicitly refers to the presence or absence of source populations near AES interventions (Tscharntke *et al.* 2005). Increased landscape complexity (as defined by Tscharntke *et al.* 2005) entails a higher coverage semi-natural habitat, which has been shown to contain source populations of a wide variety of species groups (e.g. butterflies and bumblebees: Öckinger & Smith 2007; bees, hoverflies and herbaceous plants: Kohler *et al.* 2008; moths: Fuentes-Montemayor, Goulson & Park 2011). In low-complexity landscapes, source populations are not available so species cannot colonise or utilise resources provided by AES interventions (Fig. 2a). On the other hand in complex landscapes biodiversity is high everywhere, even in areas that are managed without AES interventions (Fig. 2a, Tscharntke *et al.* 2005). As a result the benefit of AESs, that is the difference in biodiversity between areas with and without interventions, is thought to be greatest in landscapes of intermediate complexity (Fig. 2b).

Both of the perspectives outlined above have formed the basis of empirical tests, and evidence about the effects of the landscape context is summarised below. However, it is useful to note some strengths and weaknesses of these two perspectives from the outset. One weakness of inferences based on the relationship between land-use intensity and biodiversity (Fig. 1) stems from the assumption of causality. Biodiversity decreases as agricultural intensity increases (Kleijn *et al.* 2009), but decades of habitat restoration studies clearly demonstrate that reducing intensity leads to unpredictable outcomes for biodiversity (Suding, Gross & Houseman 2004). However, the perspective of Kleijn & Sutherland (2003) does allow a wide variety of AES interventions and farming systems to be quantified based on a single universal characteristic (e.g. nitrogen inputs, Kleijn *et al.* 2009; Foley *et al.* 2011).

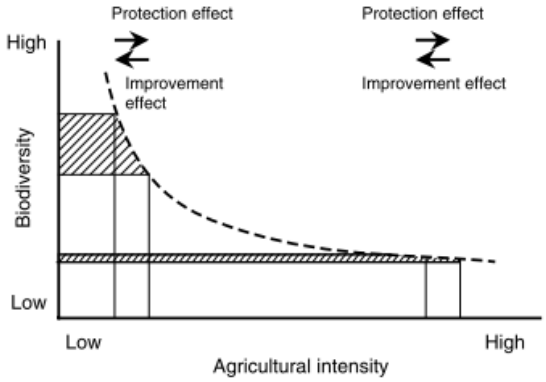


Figure 1. Proposed relationship between biodiversity and agricultural intensity. AES interventions might benefit biodiversity by decreasing intensity ("improvement effects"), or preventing increases in intensity ("protection effects"). The shape of the relationship between biodiversity and agricultural intensity is thought to be negative and exponential (Kleijn et al. 2009). It could result that benefits of AES interventions would be greater on more extensively farmed land. Taken from Kleijn & Sutherland (2003).

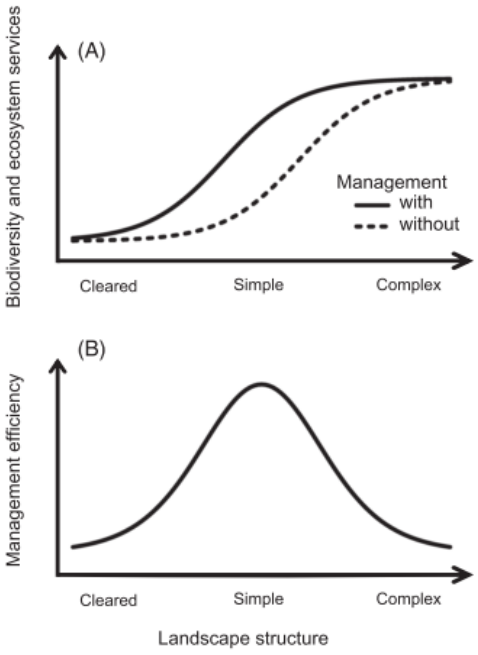


Figure 2. (a) Proposed relationship between biodiversity on farmland with (solid line) and without (dashed line) AES interventions, and the structure of the surrounding landscape. Increasing complexity usually represents a higher proportion of semi-natural habitat in the surrounding landscape (Tscharntke et al. 2005). (b) The relationship between management efficiency, i.e the biodiversity benefits of AES interventions, and the structure of the surrounding landscape. The black line here represents the absolute difference between the two lines presented in (a). Taken from Tscharntke et al. (2012).

One weakness of inferences about the benefits of AES interventions as a function of landscape complexity (Fig. 2) is that they are strongly affected by spill-over of individuals onto unsuitable agricultural fields. Thus, AES interventions in complex landscapes could appear to have low benefits for biodiversity, even if they make a substantial contribution to species' population demographics (Kleijn *et al.* 2011). Nevertheless, the landscape complexity perspective explicitly compares biodiversity on sites with, and sites without, AES interventions (Fig. 2, Tscharntke *et al.* 2005). This has proven to be a somewhat useful property, as a large number of studies have emerged that empirically test the relationship between AES benefits and features of the surrounding landscape (Heard *et al.* 2007; Batáry *et al.* 2011; Scheper *et al.* 2013; Alison *et al.* 2016).

1.8. Evidence of the effects of landscape context on the biodiversity benefits of AES interventions

One key study has characterised the shape of the relationship between biodiversity and agricultural intensity: Kleijn *et al.* (2009) modelled the relationship between plant species richness and annual nitrogen input on grasslands and arable fields using data from six European countries. The best fitting models tended to predict exponential declines in biodiversity with increasing land-use intensity, validating the hypothesis originally put forward by Kleijn & Sutherland (2003). The authors thus suggested that benefit to cost ratio of AESs would be greater in extensively farmed landscapes, although I note that this is subject to a direct causal relationship between land-use intensity and biodiversity. Furthermore, while biodiversity may decline exponentially with land-use intensity at the field-scale, it is unclear whether this relationship takes the same shape at the landscape-scale. Nonetheless, Phalan *et al.* (2011) obtained a similar result whereby the density-yield function for bird and tree species in $1km^2$ landscapes in Ghana and Northern India were often negative-trending and convex, confirming the prediction of Green *et al.* (2005). While studies of density-yield relationships and studies of biodiversity-intensity relationships are not equivalent, both conclude that

565 conservation efforts may be best focussed towards areas that already have high
566 biodiversity.

567 In contrast with the relationship between biodiversity and land-use intensity, the
568 relationship between AES benefits and elements of landscape complexity has been the
569 subject of a number of landscape-scale field studies. For example, Rundlöf & Smith
570 (2006) found that organic farming only significantly increased butterfly species richness
571 and abundance in homogenous landscapes (i.e. landscapes which comprised large arable
572 fields with little pasture). On the other hand, Concepción, Díaz & Baquero (2008)
573 summarised many variables about landscape complexity using a principal components
574 analysis, and looked for corresponding variation in the effectiveness of AESs. They
575 found mixed effects of landscape complexity on the benefits of AESs, depending on the
576 species group or aspect of landscape complexity that was considered. However, most
577 studies since have focussed on semi-natural habitat as the key aspect of landscape
578 complexity. For example, Concepción *et al.* (2012) looked at landscape complexity in
579 terms of the length of semi-natural boundaries and the proportion of unfarmed habitats.
580 For a large dataset of bees, birds, plants and spiders across six European countries, the
581 authors found that AES interventions quite consistently caused the greatest increase in
582 species richness at intermediate landscape complexities.

583 While field studies have provided useful case-studies, two recent high-profile
584 meta-analyses now form the core of evidence about how coverage of semi-natural
585 habitat affects the benefits of AES interventions (Batáry *et al.* 2011; Scheper *et al.*
586 2013). Batáry *et al.* (2011) collated data on increases in abundance and species richness
587 of a variety of plants and animals caused by AES interventions. They found that AES
588 interventions had a positive effect on species richness and abundance overall. However,
589 in croplands AES interventions only increased species richness in "simple" landscapes
590 with less than 20% semi-natural habitat within a 1km radius. Furthermore, the authors
591 found that for a subset of species considered to be pollinators it did not matter whether
592 AESs were implemented in cropland or grassland; either way benefits were greater in
593 simple landscapes. However, it is worth noting that ~75% of observations in this study

corresponded to organic farming, so many types of AES intervention were probably under-represented (Batáry *et al.* 2011).

The second meta-analysis focussed solely on pollinating insects (Scheper *et al.* 2013). As with the study of Batáry *et al.* (2011), AES interventions had significant positive effects on abundance and species richness. Another striking similarity to the previous meta-analysis was that benefits of AES interventions for pollinators were again highest in "simple" landscapes. However, Scheper *et al.* (2013) also found that benefits were non-significant in "cleared" landscapes with <1% coverage of semi-natural habitat, which lines up well with the intermediate landscape-complexity hypothesis of Tscharntke *et al.* (2005, Fig. 2). AES interventions were also less beneficial on grassland than on cropland, which could be because even intensive grassland provides non-negligible resources for pollinators. Interestingly, the authors also tested for a relationship between nitrogen inputs on control fields and the biodiversity benefits of AES interventions. They found no significant relationships, and expressed doubt about whether pollinator biodiversity declines with land-use intensity are truly exponential. However, I do not consider this to be an appropriate test of the land-use-moderated conservation effectiveness hypothesis, which considers biodiversity benefits as a function of *change* in agricultural intensity (Fig. 1, Kleijn & Sutherland 2003).

The coverage of semi-natural habitat is clearly a useful predictor of the benefits of AES interventions. However, many studies have also successfully used the proportion of arable land, which could be considered the inverse of landscape complexity (Tscharntke *et al.* 2005), to predict the benefits of AES interventions. For example, Heard *et al.* (2007) found that the benefits of sown forage patches for bumble-bees increased with the proportion of arable land within 1km. Furthermore, a follow-up study directly linked increased benefits of forage patches to reduced availability of herbaceous forbs within 1km (Carvell *et al.* 2011). The authors suggested that bumble-bees were exploiting AES interventions more where alternative resources from semi-natural habitat were not available (i.e. 'concentration' effects were stronger on more isolated AES interventions, Heard *et al.* 2007; Carvell *et al.* 2011; Kleijn *et al.* 2011). Nonetheless,

concentration effects may not have been the only mechanism at play. A later field study by Scheper *et al.* (2015) found that the benefits of wildflower strips for bumble-bees were enhanced in landscapes with a higher prevalence of early-season floral resources, such as those provided by oilseed rape. Mass-flowering crops have been shown to be a better predictor of bumble-bee densities than semi-natural habitat (Westphal, Steffan-Dewenter & Tscharntke 2003), so it is possible that spill-over occurs from mass-flowering crops to wildflower strips (but see Carvell *et al.* 2011). Interestingly, Scheper *et al.* (2015) found a similar result for solitary bees as had been reported elsewhere for bumble-bees (Carvell *et al.* 2011): Benefits of wildflower strips decreased with increasing prevalence of late-season floral resources.

1.9. Where should agri-environment schemes be placed to achieve their ultimate objectives?

The aim of AESs is to enhance biodiversity so as to contribute to two ultimate objectives: (1) to benefit species that are threatened or of conservation concern and (2) to deliver a wide variety of sustainable ecosystem services (Kleijn *et al.* 2011; Ekroos *et al.* 2014). A few studies have explicitly linked AES interventions to achievement of these ultimate objectives (e.g. Albrecht *et al.* 2007; Pywell *et al.* 2012). However, to my knowledge only two studies have linked AES benefits for rare or threatened species or provision of ecosystem services to the landscape context (Perkins *et al.* 2011; Winqvist *et al.* 2011). Perkins *et al.* (2011) found that when AESs were targeted towards existing breeding populations of corn bunting *Emberiza calandra*, they lead to local increases in the population trend of this severely declining bird species. I echo others in commending this study for directly testing the effects of spatial targeting of AES interventions on population dynamics of a threatened species (Whittingham 2011; Kleijn *et al.* 2011). On ecosystem services, Winqvist *et al.* (2011) found interacting effects of organic farming and landscape complexity on aphid mortality. The authors found that the potential for biological control was greatest on organic fields in landscapes with a low coverage of arable land.

Nonetheless, many studies have investigated the outcomes of AES interventions for threatened species and ecosystem services. It has been established that evidence-based AES interventions can benefit rare or threatened species (Pywell *et al.* 2012), but non-tailored interventions such as maintaining hedgerow trees also have some potential in that respect (Merckx *et al.* 2010b). Furthermore, a few studies have linked AES interventions to population level benefits to threatened species, not just increases in local species richness or abundance (Perkins *et al.* 2011). For example, Baker *et al.* (2012) found that AES winter food resources increased the population growth rates of farmland bird species, many of which are declining across Europe (Gregory *et al.* 2008). Some studies have also directly linked AES interventions to the provision of ecosystem services (but see Brittain *et al.* 2010). For example, Albrecht *et al.* (2007) found that extensively-managed hay meadows increased the species richness and abundance of small-sized pollinators in nearby intensive grassland, increasing the fruit-set of experimentally placed radish plants *Raphanus sativus*. Another study found that organic farms had a high community-evenness of biological pest control agents, which caused a decrease in the abundance of pests and an increase in crop yield of potatoes *Solanum tuberosum* (Crowder *et al.* 2010). However, ecosystem services on AES interventions have also been inferred from the abundance of the agents which provide them, for example aphidophagous syrphid flies (Haenke *et al.* 2009). The accumulating evidence that AESs provide ecosystem services may help to explain results from a recent study in which created wildlife habitats did not lead to a decrease in yield at the field scale (Pywell *et al.* 2015).

This evidence base has facilitated the production of a few provisional guidelines on the optimal placement of AES interventions (Kleijn *et al.* 2011; Ekroos *et al.* 2014). Kleijn *et al.* (2011) produced guidelines based on assumptions that (1) species of conservation concern are mostly restricted to the most extensively farmed areas, (2) ecosystem services have greater potential benefits in intensively farmed areas and (3) the majority of ecosystem services are provided by common species (Kleijn *et al.* 2015; Winfree *et al.* 2015). The authors argued that when the objective is to benefit rare or threatened species, AES interventions should be placed in agriculturally marginal areas

that have high biodiversity and are close to source populations. On the other hand when the objective is to increase ecosystem services, AES interventions should be placed in more intensively farmed landscapes independent of source populations; common species are generally able to colonise all but the most isolated sites (Kleijn *et al.* 2011). More recently, Ekroos *et al.* (2014) produced a model based on a similar set of assumptions to those outlined above, considering two types of AES intervention: the first creates non-crop habitat to benefit both threatened species and ecosystem service providers, and the second reduces agricultural intensity to benefit ecosystem service providers only. This model demonstrated that the optimal strategy to increase agricultural productivity while maintaining biodiversity could include a balance of the two intervention types (Ekroos *et al.* 2014).

1.10. Toward optimal placement of agri-environment schemes

While some studies of AESs have had severe shortcomings, not least a lack of control data (Kleijn & Sutherland 2003), significant progress has been made in understanding how the landscape context mediates the benefits of AES interventions for biodiversity. Nonetheless, the advice that can be provided on optimising AESs is still limited due to significant evidence gaps (Kleijn *et al.* 2011). For example, too few studies link AES interventions to aspects of biodiversity which are of conservation concern or which provide ecosystem services (Kleijn *et al.* 2011). Of these studies, too few take the landscape context into consideration. Furthermore, future studies might consider the effects of AESs across larger spatial and temporal scales (Whittingham 2011). Such research would allow more robust conclusions about whether AESs contribute to regional or global targets on biodiversity (Kleijn *et al.* 2011). Most AES interventions are implemented on small patches of land, such that large-scale effects are not necessarily expected to occur (Whittingham 2007). However, a few studies have shown benefits of organic farming for butterflies at both local- and landscape-scales (Rundlöf, Bengtsson & Smith 2007; Hodgson *et al.* 2010).

Studies of AES interventions have been criticised on the basis that they tend to focus on changes in local abundance and species richness. This means that results are

susceptible to small-scale spill-over and concentration effects, and do not necessarily reflect local birth rates and death rates (Kleijn *et al.* 2011). Nonetheless, the behavioural responses of individuals to AESs can be just as relevant as population-level responses for the provisioning of ecosystem services. There may be considerable potential for "win-win" outcomes of AES interventions for biodiversity and agriculture (Bommarco, Kleijn & Potts 2013; Pywell *et al.* 2015), and ecosystem services on farmland may depend on common species (Winfree *et al.* 2015). As such, perhaps it is apt that many studies have focussed on local changes in abundance rather than the population demographics of rare species (Scheper *et al.* 2013). While more studies are needed which link AESs to their ultimate objectives, studies of raw effects on abundance and diversity have been and will continue to be worthwhile. This is because values attributed to species and individuals, whether based on ecosystem services or extinction risk, will vary over time and between stakeholders. If studies report raw effects on abundance and species richness, unbiased policy-relevant information can still be collated at a later stage through systematic reviews and synopses (Dicks *et al.* 2015, 2016).

A running theme of recent studies and commentary on AESs is the division of schemes into those which aim to benefit species of conservation concern and those which aim to provide ecosystem services (Kleijn *et al.* 2011; Ekroos *et al.* 2014; Merckx & Pereira 2015). Merckx & Pereira (2015) go so far as to propose that on marginal land, subsidies should involve large-scale managed succession or "rewilding". On the other hand, on fertile land subsidies should encourage aspects of biodiversity that are compatible with agricultural systems and may even help to increase yield (Merckx & Pereira 2015). Such an approach could balance demand for food with conservation of biodiversity (Phalan *et al.* 2011), while considering the potential for positive feedbacks of ecosystem service providers on yields (Bommarco, Kleijn & Potts 2013; Ekroos *et al.* 2014). However, before such policies are put into practice, more research is needed to determine the feasibility of rewilding and the extent to which it benefits biodiversity (see Appendix P1 for overview and discussion of rewilding in a UK context). Furthermore, on the subject of ecosystem services, questions remain about how service provision scales with the abundance and diversity of service providers (Cardinale *et al.* 2012).

740 Finally, understanding about the net benefits of AESs is limited (Hodgson *et al.* 2010).
741 Future studies should determine where in the landscape the immediate cost of AESs may
742 be most clearly offset by demand for ecosystem services (Ekroos *et al.* 2014).

Chapter 2: Spatial targeting of habitat creation has the potential to improve agri-environment scheme outcomes for macro-moths

A version of this chapter was published in 2016 in the *Journal of Applied Ecology* (Alison *et al.* 2016). Jamie Alison and Jenny Hodgson designed the study with help and feedback from Simon Duffield, Mike Morecroft and Rob Marrs. Jamie Alison and Simon Duffield sought ground-truth for data on AES interventions in Hampshire and later secured permission for macro-moth surveys. Jamie Alison conducted the field work and data analysis and wrote the manuscript. Simon Duffield, Catharina van Noordwijk, Mike Morecroft, Rob Marrs, Ilik Saccheri and Jenny Hodgson provided feedback on the manuscript.

2.1.Abstract

Agri-environment schemes (AES) are a major avenue for habitat creation and restoration across Europe. To maximise benefits for biodiversity, AES interventions are sometimes spatially targeted relative to existing semi-natural habitat (SNH). However, the evidence base for effective spatial targeting is deficient; studies until now have collated data across several taxa and regions, resulting in nonspecific advice that is only useful at the regional scale. I present a field study using macro-moths (Lepidoptera) to test (a) the impact of creating grassland habitat on arable field margins, (b) how the impact of this type of AES intervention varies according to species specialism and (c) the potential impact of spatially targeting AES interventions for proximity to semi-natural calcareous grassland (CG). I surveyed macro-moths on arable fields with and without AES interventions across a range of levels of connectivity to CG. I also surveyed macro-moths on CG habitat. Macro-moth abundance was highest on CG and lowest on arable field centres. The benefits of AES interventions were largest for grassland-associated macro-moths: abundances were ~1.4 times higher on AES margins than control margins for this group. CG-associated macro-moths only benefited from AES interventions that were close (<1 km) to large areas (>10 ha) of CG habitat. I estimate that clustering AES interventions around CG could lead to a ~17% increase in CG macro-moth abundance on arable margins across my sampled region, leading to an overall increase of 2.6% within the sampled region. I provide evidence that for conservation of species associated with a specific type of semi-natural habitat (SNH), agri-environment scheme (AES) interventions are most effectively positioned close to that habitat. My study on macro-moths in arable fields with and without AES interventions across a range of levels of connectivity to calcareous grassland represents a template for the production of tailored spatial targeting advice. I show that optimal positioning of AES habitat creation depends on the extent of SNH in the surrounding landscape as well as the ecology and life history of species being conserved.

2.2.Introduction

The spread and intensification of agricultural land-use has been the major cause of biodiversity declines (Balmford, Green & Phalan 2012) and this has negative implications for human welfare (MEA 2005). To make farmland less hostile for wildlife, governments use various forms of agri-environment scheme (AES) to give farmers financial incentives for habitat creation and restoration. One widespread example is the creation of grassland strips around arable fields through sowing a grass mix or natural regeneration. These strips have benefits for local biodiversity (Merckx *et al.* 2012; Pywell *et al.* 2012) and don't necessarily decrease crop yield at the field scale (Pywell *et al.* 2015). AES interventions can benefit wildlife, but funding for such measures is limited; the European Union spend over €3 billion per year on AES management, which represents ca. 6% of annual expenditure under the Common Agricultural Policy (European Commission 2015). Given the scale of these investments, it is vital that land managers and governmental bodies use all the tools at their disposal to make AESs as effective as possible.

Biodiversity benefits of AESs are highly dependent on the extent of existing semi-natural habitat (SNH) in the surrounding landscape (Tscharntke *et al.* 2005). For example, many recent studies show increased wildlife benefits of AES interventions where there is intermediate coverage of SNH nearby (Batáry *et al.* 2011; Concepción *et al.* 2012; Scheper *et al.* 2013). This makes ecological sense; the breeding and foraging resources provided by AESs may be insufficient to maintain independent populations (Whittingham 2007), whilst protected SNH supports high densities of the majority of species (Gillingham *et al.* 2014) and acts as a population source for nearby farmland (e.g. butterflies and bumble-bees: Öckinger & Smith 2007; bees, hoverflies and herbaceous plants: Kohler *et al.* 2008; Fuentes-Montemayor, Goulson & Park 2011). As such, farmland that is close to high-quality habitats has been associated with increased floral visitation rate by native pollinators (Ricketts *et al.* 2008) and increased fruit-set of some types of agricultural plants (Albrecht *et al.* 2007). An alternative perspective of the biodiversity benefits of SNH can be seen through biodiversity declines associated with

agricultural intensification. For example, the abundance of nationally declining macro-moth species is lower where there is greater arable land cover within a 0.8km radius (Merckx *et al.* 2012). AESs are probably most effective in landscapes with intermediate coverage of SNH because AES resources that are very isolated from SNH cannot be colonised or utilised fully, whist AES resources adjacent to large areas of SNH are to some extent redundant (Tscharntke *et al.* 2005).

Spatial targeting relative to SNH clearly has potential to increase biodiversity gains per unit investment in AESs. However, the information that is currently available can only direct the allocation of AES interventions in a very broad sense. For example, a recent meta-analysis showed that wildlife benefits of AES interventions were largest in croplands with 1-20% coverage of SNH within 1km (Scheper *et al.* 2013). This result has potential to inform spatial targeting of AESs at the regional scale, but is probably not useful to inform spatial targeting across one or a few farm holdings.

Furthermore, the few published studies assessing the interaction between AESs and SNH collate data across several taxa, regions and types of AES intervention (Batáry *et al.* 2011; Concepción *et al.* 2012; Scheper *et al.* 2013). Conservation objectives usually prioritise specific habitat types or subsets of species; in England, AESs have been targeted to benefit "nationally important" habitats and species (NE 2014a). However, there is a lack of clarity about (1) where to put AES interventions relative to specific types of SNH to maximise biodiversity benefits, and (2) which species groups will benefit most from this spatial targeting.

I carried out a field study of macro-moths (Lepidoptera) to assess the potential for spatial targeting to improve biodiversity outcomes from AESs. Macro-moths are an appropriate indicator taxon because they are species-rich, are major nocturnal pollinators, have known habitat associations and have shown population level responses to environmental change in the UK (Waring & Townsend 2009; Macgregor *et al.* 2014; Fox *et al.* 2014). I focus on AES interventions that create small areas of grassland habitat on arable field margins, and I consider the extent of nearby SNH in the form of calcareous grassland (CG). Calcareous grassland is a priority habitat in the UK which is

particularly important for declining macro-moth species, because the larvae of declining moths tend to feed on plants adapted to open, nutrient poor habitats (Fox *et al.* 2014).

I surveyed arable field margins with AES interventions (treatment) and without AES interventions (control) across a range of connectivity to CG. I also surveyed high-quality CG habitat and arable field centres. To my knowledge this is the first study to simultaneously survey macro-moths on protected semi-natural grasslands as well as arable land with and without AES interventions. I tested the hypotheses that (1) macro-moth abundance on treatment margins is lower than on CG habitat, but higher than on control margins or arable field centres, (2) the impact of AES interventions depends on the habitat association of the macro-moth species in question and (3) for macro-moths associated with CG habitat, the increase in abundance on treatment margins vs control margins is greater when situated at higher connectivity to CG. Finally, taking into account the constraints of the landscape, I estimate how spatial targeting would influence AES outcomes for CG macro-moths in my study region.

2.3.Methods

2.3.1. Site selection

Spatial analyses for site selection were carried out in ArcMap 10.1 (ESRI, Redlands, California) using five geographic datasets (see Appendix A1 for details). Four study landscapes were selected within north-west Hampshire, central southern England (Fig. 3, top and middle). Each landscape was adjacent to a large (>10ha) patch of CG at least partially contained in a Site of Special Scientific Interest (SSSI, UK conservation designation); ultimately, there was a 3.7% coverage of CG habitat within a 1km buffer of all moth survey locations. Landscapes also had >50% coverage of arable land extending approximately 3km from the CG patch. Samples could thus be taken at a range of connectivity to CG habitat whilst minimising confounding effects of non-arable, non-CG land-use types. Landscapes contained holdings in Higher Level Stewardship (HLS, top-tier AES in England, NE 2013) to provide an adequate number of accessible arable fields both with and without AES interventions. The holdings I

867 surveyed were not receiving payments for organic management. I defined an "AES
868 intervention" in this chapter as AES-funded management that creates an area of
869 grassland at least 6m wide on the margin of an arable field. In each landscape, the most
870 common type of AES intervention was studied (6m buffer strips in landscapes a, c & d,
871 nectar flower mixes in landscape b; see Fig. 3 for locations of landscapes and Table A1
872 for management details).

873 I quantified the extent of CG around a given point in space using a connectivity
874 metric that combined information on both distance to and areas of all known habitat
875 patches. I used a negative exponential kernel weighted by CG habitat area (see
876 Appendix A2), and calculated a continuous surface of connectivity to CG across
877 Hampshire at 100m resolution. This connectivity metric was chosen as it outperforms
878 simpler metrics when predicting colonisation events in fragmented landscapes
879 (Moilanen & Nieminen 2002).

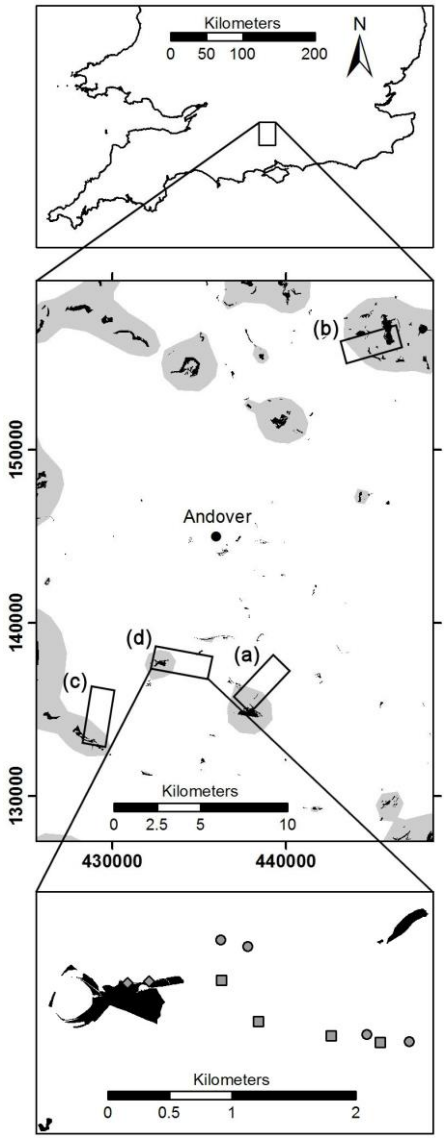


Figure 3. (top) The location of the study region on the island of Great Britain. (middle) Locations of the four study landscapes (a-d) near the town of Andover in north-west Hampshire, central-southern England. Coverage of calcareous grassland habitat (black polygons) was obtained from the Hampshire Biodiversity Information Centre (HBIC) and Natural England. The area coloured grey has relatively high connectivity to calcareous grassland habitat (above the median connectivity of macro-moth survey locations in this study, calculated as in Appendix A2). All-numeric coordinates from Great Britain's Ordnance Survey (OS) National Grid are displayed. The latitude and longitude at the centre of this map is approximately 51°12′10″N 01°27′26″W. (bottom) Close-up view of ten survey locations in landscape (d): two on calcareous grassland habitat (grey diamonds), four on arable fields with agri-environment scheme interventions (grey squares) and four on arable fields with control margins (grey circles). Not shown here are eight more survey locations that were 45m toward the centres of the arable fields. Contains information from OS licensed under the Open Government License v3.0.

2.3.2. Macro-moth surveys

Macro-moth surveys were carried out at 18 survey locations in each landscape (see Appendix A3 for macro-moth survey protocol). Two of 18 survey locations were on CG habitat. The remaining 16 were on the margins and centres of four pairs of large arable fields, spanning the full gradient of connectivity to CG in the landscape (fields >5ha, crops primarily wheat and barley, nectar-rich crops not in flower during surveys). In each pair of fields, one field contained a treatment margin (AES intervention present) and the other contained a control margin (crop cover extends to within 2m of field boundary). Survey locations on arable fields were always situated so that the nearest field boundary backed onto another arable field. In the case of control margins, an AES intervention was not present on either side of that boundary. As well as being physically close (within 1km) and having similar connectivity to CG, the fields in a treatment-control pair were matched where possible on within-field crop (in 8 of 16 cases) and hedge structure (absent, <3m in height or >3m, matched in 12 of 16 cases, hedgerow present on 30 of 32 margin survey locations).

Landscapes were visited one at a time between June 2nd and July 22nd 2014, with each being surveyed for macro-moths for six consecutive good weather nights (Appendix A3). Each night, ten light traps were used to simultaneously sample one survey location on each of the eight arable fields and two survey locations on the CG (as in the bottom panel of Fig. 3). On arable fields, traps were alternated between a margin survey location (placed 5m from the boundary for nights 1, 3 and 5) and a centre survey location (45m from the boundary for nights 2, 4 and 6). Within the CG habitat there was no margin/centre distinction, so survey locations were surveyed twice as often. Sampling simultaneously across an entire landscape minimised confounding between my variables of interest and intrinsic night-to-night variation in macro-moth abundance associated with weather and moonlight (McGeachie 1989).

Moths were identified and released on site. To minimise recaptures of moth individuals, on subsequent visits to a given survey location I placed the moth trap at least 50m from the previous point of survey. This was done so that the attraction radius

of light traps did not include any point where moths had been released within the last two good weather nights (Merckx & Slade 2014).

2.3.3. Data analysis

All statistical analyses were carried out in *R* 3.0.3 (R Core Team 2017). On arable fields, abundance was calculated for each macro-moth species as the sum of counts across the three samples (= trapping occasions) in each survey location in each landscape. CG survey locations were surveyed twice as often as arable survey locations, and comprised six samples. For this reason, each CG survey location was divided into two sets of three samples: one set for when arable fields were surveyed at the margin on the same night, and one for when they were surveyed at the centre. This resulted in a total of 80 observations (64 arable and 16 CG) per species (180 species) summing to 14,400 observations overall.

The abundance of each macro-moth species was used as the response variable in generalised linear mixed models (GLMMs) with Poisson error structures (log link) in the package *lme4* (Bates *et al.* 2014). There was a high level of non-independence in the data caused by spatial and temporal autocorrelation, and by observations of 180 species being drawn from each individual survey location. Furthermore, each species varied in abundance between landscapes according to its phenology and its geographic distribution. To account for these sources of non-independence, random intercepts were included for field, dates of survey, and species identity nested within landscape. A random intercept was also included for each data point in order to model extra-Poisson variation that was present in the data. Observation-level random effects have been shown to be a simple and robust way to account for overdispersion in count data (Harrison 2014).

Three variables were used as fixed effects in GLMMs: “species specialism”, “management” and “connectivity to CG”. “Species specialism” was the result of classifying macro-moth species as either CG species, grassland species, or other species using a guidebook (Waring & Townsend 2009, see Appendix A3 for criteria).

"Management" was a composite of three incompletely crossed factors, and I use "management$_{full}$" as shorthand for the complete set of 5 possible levels: CG, AES intervention, control margin, arable field centre near AES intervention and arable centre near control margin. When testing for effects of "management", I always produced models with simpler nested versions of this variable; "management$_{AES}$" (4 levels: CG, AES intervention, control margin, arable centre) assumes no effect of AES interventions at the centres of fields, whilst "managment$_{margin}$" (3 levels: CG, arable margin, arable centre) assumes no effect of AES interventions at all. "Connectivity to CG" of each survey location was extracted from the connectivity metric produced during site selection (Appendix A2) using the *R* package *maptools* (Bivand & Lewin-Koh 2014). This variable was $\log_2$ transformed and centred on the mean prior to model fitting to ensure model convergence.

To test hypothesis (1) that moth abundance on AES interventions was different from other management types, I produced GLMMs using forms of the "management" variable to predict the abundance of all species of macro-moths. To test hypotheses (2) that impact of AES interventions depend on species' habitat associations and (3) that for CG macro-moths the impact of AES interventions increases with connectivity to CG, GLMMs were produced using fixed effects of "species specialism", "management" and "connectivity to CG" allowing all possible interactions. Model selection was carried out using an information theoretic approach based on Akaike's Information Criterion (AIC, Burnham & Anderson 2002). Following Richards (2008), I report models with $\Delta AIC \leq 6$ except those with a higher AIC than any simpler nested version. For the lowest AIC models, I used Wald *Z*-tests in the package *lme4* (Bates *et al.* 2014) to determine whether individual parameters differed significantly from zero.

For CG macro-moths, I explored the potential impact of spatially targeting AES interventions close to CG habitat. To do this, I divided land in Hampshire into four categories of connectivity to CG (henceforth referred to as "connectivity bands": $C < -2$, $-2 \leq C < 0$, $0 \leq C < 2$, and $C \geq 2$). These connectivity bands were selected such that each of the four bands would contain at least one of the AES interventions and one of the

control margins that I surveyed. Using the lowest AIC model, I predicted CG macro-moth abundance corresponding to four management types (CG, AES intervention, control margin and arable centre) at four levels of connectivity to CG (corresponding to the four connectivity bands: -3,-1,1 and 3). I then multiplied those predictions by the area of each management type in each of the four connectivity bands.

The process of multiplying predicted CG macro-moth abundances by corresponding areas was carried out twice; in the first instance areas were calculated under the existing distribution of AES interventions in Hampshire (status quo). In the second instance, areas were calculated under a hypothetical scenario with maximum spatial targeting of AES interventions towards CG (targeted). This targeted scenario redistributed the same total area of AES interventions across Hampshire, giving priority to arable field margins in the highest band of connectivity to CG (see Appendix A4 for more details). During this process, I allowed AES interventions to fill arable land up to 10m from the field boundary. This was to strike a balance between the widths of the two types of AES intervention that I surveyed; 6m buffer strips were consistently 6m wide, whereas nectar flower mixes were up to 20m wide.

2.4.Results

7228 macro-moth individuals of 180 species were captured and identified from 240 light trap samples (Table A2). 7.8% of those individuals belonged to 15 species that were determined *a priori* to be associated with CG habitat, whilst 15.9% of individuals belonged to 24 species associated with other grassland habitat. The remaining 76.3% of individuals belonged to 141 species that were either associated with other habitats, such as woodland, or of no strong habitat association. There was a substantial overlap in species composition of protected CG and surrounding farmland; of the 125 species captured on CG throughout the study, 106 were also captured on arable fields (see Table A6 for full species list and their abundance on different management types).

Considering all species, and without considering connectivity to CG, the abundance of macro-moths was lowest on arable field centres, intermediate on arable

1010 field margins, and highest on CG (Fig. 4a, Table A2). A model using management$_{AES}$ as
1011 the sole independent variable outperformed a model with management$_{margin}$ (models 33
1012 and 41, Table A5, ΔAIC = 3.71). The model with management$_{AES}$ also outperformed a
1013 model with management$_{full}$ (models 33 and 37, Table A5, ΔAIC = 1.90). Following
1014 Richards (2008), the model with management$_{full}$ was omitted because its AIC was higher
1015 than that of the simpler nested version. The management$_{AES}$ model was thus the best of
1016 the three models, and the parameters of this model reveal that the overall abundance of
1017 macro-moths on AES interventions was 1.23 times greater than on control margins (P =
1018 0.017, Fig. 4a, Table A3). Macro-moth abundance was also 1.31 times greater on CG
1019 than on AES interventions (P = 0.033, Fig. 4a, Table A3) and 2.94 times greater on AES
1020 interventions than on arable field centres (P < 0.001, Fig. 4a, Table A3).

1021 When allowing species specialism and connectivity to CG as predictors of
1022 macro-moth abundance, a best model emerged including a three way interaction with the
1023 variable management$_{AES}$ (Table 1, version with negative binomial error is in Table A7);
1024 the effect of different management types was dependent on connectivity, and this
1025 interaction between management and connectivity depended on whether the species in
1026 question was a CG species, grassland species or other species. Grassland species
1027 responded strongly to AES interventions, with abundances 1.42 times greater than on
1028 control margins (at mean connectivity to CG, P = 0.024, Table 1, see also Fig. 4c). For
1029 CG species, but not grassland species or other species, connectivity to CG had a strong
1030 positive effect on abundance overall (Fig. 5, Fig. A1). In contrast with grassland species,
1031 CG species showed a significantly shallower slope with connectivity on control margins
1032 than on AES interventions (P = 0.025, Fig. 5, Table 1). This effect means that AES
1033 interventions apparently have a more positive effect on abundance of CG macro-moths
1034 at higher connectivity to CG. One other model was supported too, and this model did not
1035 include an interaction between the effects of AES interventions and connectivity to CG
1036 (ΔAIC = 2.13, see models 1 and 2 in Table A5).

1037

Table 1. Summary of fixed effect parameters in the lowest AIC model predicting the abundance of 180 species of macro-moths (parameters = 30, Log Likelihood = -6521.29, AIC = 13098.57, ΔAIC next best = 2.13, Table A5). This generalised linear mixed model (GLMM, Poisson error, log-link) included a three way interaction between the variables managementAES (4 levels: calcareous grassland (CG), AES intervention (base level), control margin, arable centre), species specialism (3 levels: CG species, grassland species (base level), or other species) and connectivity to CG. Random intercepts were included for field, dates of survey, and species identity nested within landscape. Observation-level random intercepts were included to account for overdispersion in count data. Models were produced using the package lme4 (Bates et al. 2014) using Wald Z-tests to determine if parameters differed significantly from zero (parameters with $P < 0.05$ in bold)**.**

Species group	Parameter	Par. estimate	Std. error	*Z*	*P*(>|*Z*|)
Grassland species (associated with grassland but not calcareous grassland)	**Intercept for grassland species (on AES intervention at mean connectivity to CG)**	**-2.916**	**0.316**	**-9.240**	**<0.001**
	Arable centre	**-0.947**	**0.141**	**-6.727**	**<0.001**
	Control margin	**-0.353**	**0.156**	**-2.265**	**0.024**
	Calcareous grassland	-0.694	0.432	-1.608	0.108
	Connectivity to CG	-0.067	0.066	-1.011	0.312
	Connectivity to CG: Arable centre	**0.198**	**0.074**	**2.686**	**0.007**
	Connectivity to CG: Control margin	0.050	0.083	0.599	0.549
	Connectivity to CG: Calcareous grassland	**0.397**	**0.195**	**2.038**	**0.042**
Other species (not associated with grassland or calcareous grassland)	Intercept for other species (on AES intervention at mean connectivity to CG)	-0.624	0.327	-1.905	0.057
	Arable centre	-0.083	0.148	-0.559	0.576
	Control margin	0.181	0.161	1.129	0.259
	Calcareous grassland	**1.477**	**0.356**	**4.150**	**<0.001**
	Connectivity to CG	0.072	0.063	1.155	0.248
	Connectivity to CG: Arable centre	-0.086	0.081	-1.057	0.290
	Connectivity to CG: Control margin	-0.013	0.086	-0.153	0.879
	Connectivity to CG: Calcareous grassland	**-0.715**	**0.160**	**-4.461**	**<0.001**
Calcareous grassland (CG) species (associated with calcareous grassland)	**Intercept for CG species (on AES intervention at mean connectivity to CG)**	**-1.180**	**0.508**	**-2.322**	**0.020**
	Arable centre	-0.461	0.288	-1.602	0.109
	Control margin	0.217	0.276	0.787	0.431
	Calcareous grassland	0.491	0.663	0.741	0.459
	Connectivity to CG	**0.535**	**0.131**	**4.088**	**<0.001**
	Connectivity to CG: Arable centre	0.191	0.181	1.061	0.289
	Connectivity to CG: Control margin	**-0.384**	**0.171**	**-2.246**	**0.025**
	Connectivity to CG: Calcareous grassland	-0.097	0.288	-0.338	0.735

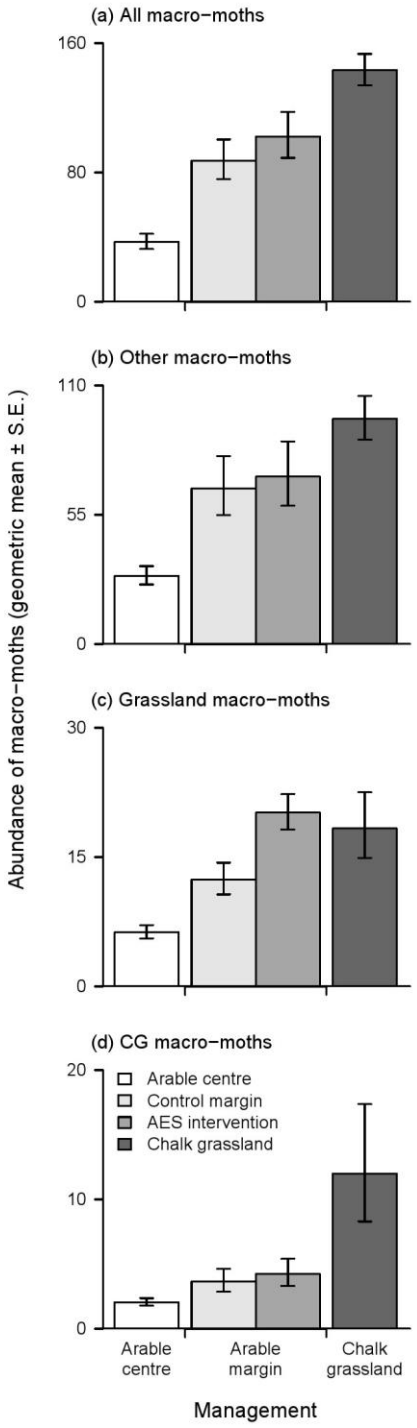


Figure 4. Geometric means ± standard errors of the abundance of (a) all macro-moths (180 species), (b) other macro-moths (141 species), (c) grassland macro-moths (24 species) and (d) calcareous grassland (CG) macro-moths (15 species) across survey locations (summed across 3 trapping nights) on each of four land management types: CG habitat (n = 16), arable field centres (45m from field boundary, n = 32), AES interventions (5m from boundary, AES intervention present, n = 16) and control margins (5m from boundary, no AES intervention present, n = 16).

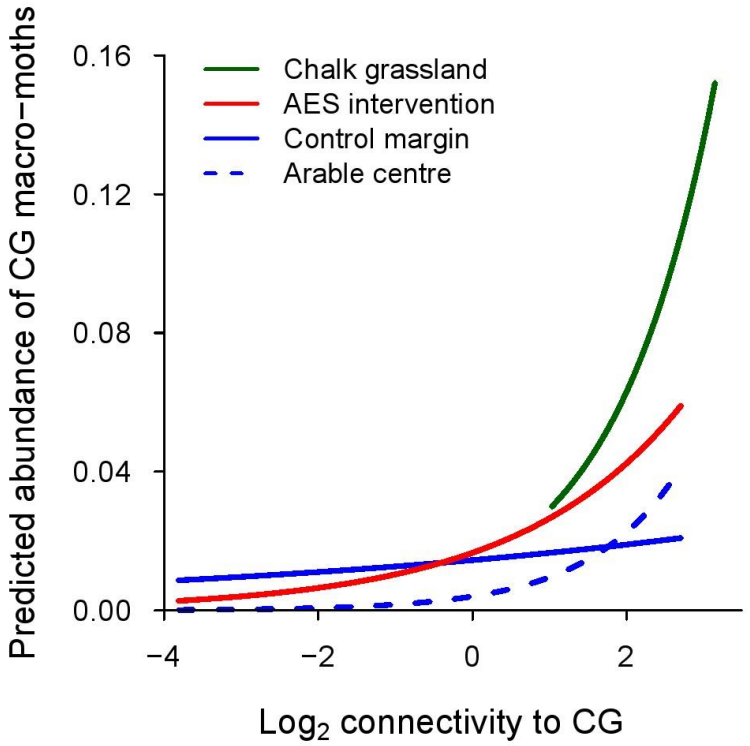


Figure 5. Model-fitted abundance of calcareous grassland (CG) macro-moths (15 species) across a range of connectivity to CG on each of four land management types: CG, AES interventions, control margins and arable field centres. Predicted abundance represents the number of individuals of the average CG species across three trapping nights. A high value of connectivity to CG means that a site was closer to larger areas of CG habitat (Appendix A2). Connectivity to CG of zero represents the mean connectivity to CG of macro-moth survey locations in this study. Predictions were produced using the generalised linear mixed model (GLMM) detailed in Table 1, using the range of connectivity to CG that was observed for each management type. Similar figures for "grassland" and "other" species are provided in Fig. A1.

I predicted the relative abundance of CG macro-moths under a hypothetical scenario whereby AES interventions were maximally targeted to be close to CG habitat (targeted scenario, Table A4). I compared predicted relative abundance under the targeted scenario with that under the existing distribution of AES interventions (status quo). Predicted relative abundance of CG macro-moths on arable margins across Hampshire was 16.9% higher under the targeted scenario than it was under the status quo. When taking into account all CG and arable land in Hampshire, predicted relative abundance of CG macro-moths was 2.6% higher under the targeted scenario than it was under the status quo.

2.5.Discussion

In support of hypothesis (1) I show that overall macro-moth abundance is higher on AES interventions than control margins, lowest on arable field centres, and highest on CG habitat. These results can be explained in light of current knowledge about the ecology and life history of Lepidoptera; abundance is affected by larval food plant availability, nectar sources for adults, presence of landmark features and shelter (Pywell *et al.* 2004b; Dover & Settele 2009). CG habitat provides all of the above because it supports exceptionally high plant biodiversity, including occasional trees and shrubs (Diacon-Bolli *et al.* 2012). In contrast, the centres of arable fields are featureless crop monocultures. Low abundance here probably corresponds to the absence of food and shelter for most macro-moth species, and in some cases harmful chemical inputs (e.g. insecticides, see Hahn *et al.* 2015). Arable margins have intermediate macro-moth abundance, which almost certainly relates to the shelter, nectar and larval food plants provided by hedgerows and grass margins (Pywell *et al.* 2004b; Merckx *et al.* 2012).

The increase in overall macro-moth abundance on AES interventions relative to control margins in this study was small (1.23 times higher), which is unsurprising in light of similar comparisons made in previous studies. Fuentes-Montemayor *et al.* (2011) and Merckx *et al.* (2012) both found no significant increase in overall macro-moth abundance on grass margins when compared with conventionally managed alternatives, although Merckx *et al.* (2012) did find an increase in species richness.

When investigating a subset of nine common and widespread macro-moth species, Merckx *et al.* (2009a) found that abundance was 1.40 times higher on 6m grass margins than on standard margins. This resembles strikingly the increase I observed for grassland generalist macro-moths (1.42 times more abundant on AES than control margins), and part of the explanation for this might be that eight of the nine species they studied had grass or herb feeding larvae. Merckx *et al.* (2009a) also found that 6m grass margins were associated with increased macro-moth abundance at the centre of the field, but I found no such effect here.

With respect to hypothesis (2) I show that AES interventions on arable margins result in an increase in macro-moth abundance, but the size of this benefit depends on the habitat association of the species considered (Fig. 4). This provides insights into the mechanisms through which AES interventions benefit macro-moths, which could be used to improve spatial targeting guidelines. For example, here I show that benefits of AES interventions are substantial for grassland generalist species irrespective of connectivity to SNH. This is not true for CG species or other species, so I suggest that overall benefits of AES habitat creation for macro-moths are driven mainly by the provision of larval food plants. Thus, it is the grassland generalist species that largely feel the benefit of this provision; if provision of nectar or shelter were driving changes in abundance, I might expect all three groups of macro-moths to benefit to a similar extent. I can also conclude that AES interventions may provide benefits for generalist species even when they are not spatially targeted - this could satisfy the aims of a scheme if the desired outcome is the provision of ecosystem services rather than the conservation of priority species. However, it must be noted that benefits for such generalist species are predicted to be more substantial when AES interventions are implemented at larger, landscape-scales, because small-scale AES implementation mainly benefits low mobility species whilst large-scale implementation benefits both low and high mobility species (Merckx *et al.* 2009a; Merckx & Macdonald 2015).

In support of hypothesis (3) I show that CG specialist macro-moths only appear to benefit from AES interventions on arable field margins that are close to their core

habitat. I suggest that when conservationists recognise certain habitats or species as a priority (as they have done in England, NE 2014a), AES habitat creation is probably best targeted at high connectivity to those habitats. This would increase the benefits of AES interventions for specialized species, whilst also benefitting non-specialist (though generally declining, Fox *et al.* 2014) wider-countryside species. The interaction that I found, where CG macro-moth abundance increased more steeply with connectivity on AES margins, would imply that the best strategy is to cluster interventions around CG to the maximum extent possible. This by itself would be an informative guideline, but it is also interesting to predict approximately the maximum benefit that could be achieved, given that targeting is constrained by the configuration of the landscape and the total area of interventions. Based on land cover in Hampshire, I predicted that the overall abundance of CG macro-moths could be increased by 2.6% as a result of their increased abundance on field margins by 16.9%. Depending on the costs and the willingness of landowners to cooperate with targeting, this potential benefit may compare favourably with other available management options affecting CG species; these may include the creation of new areas of CG habitat. It should be noted that within a 1km buffer of all survey locations in this study, coverage of CG habitat was 3.7%. Batáry *et al*. (2011) showed that agri-environmental management is most beneficial for arthropods in "simple" landscapes with 0-20% SNH, and almost all of my arable survey locations fell into this category. It remains unclear whether spatial targeting would be effective for CG macro-moths in "complex" landscapes with very high coverage of SNH.

It could be argued that the benefits of AES interventions for CG species are surprisingly large. This is because the interventions I studied were not at all tailored towards CG species: they simply converted a small area of crop cover into grassland, and in one landscape planted flowers to increase nectar availability. One factor contributing to this result is that most of the CG species caught in this study are not overly restricted or rare (see Table A6 for a full species list), hence I was able to collect sufficient individuals to test my hypotheses. However, this is not the first time non-tailored AES interventions have been seen to benefit specialized species. For example, a

previous study reported increases in a highly endangered macro-moth species in association with AES hedgerow trees (Merckx *et al.* 2010b).

When predicting the outcome of spatial targeting, note that I am making strong assumptions that the relationships found in my statistical models will remain the same when the landscape configuration is changed. Such assumptions would not hold if connectivity interacts with other landscape variables that I did not consider. Furthermore, the effect of increasing the extent of interventions close to CG may depend on the mechanism that causes macro-moth abundance to be higher on interventions. Because of basic natural history, as well as the steepness of the relationship between connectivity and abundance, I suspect that the AES interventions in this study are not able to support independent viable populations of CG macro-moths. The AES interventions studied here probably provide plenty of nectar for adults in this group, and this is especially true for nectar flower mixes (surveyed in landscape b, Fig. 3); Carvell *et al.* (2007) found that total flower abundance was significantly greater on pollen and nectar margins than on grass margins, although the species richness of plants in flower did not differ between these two intervention types. Beyond nectar provision, I suspect that AES interventions only afford small quantities of suitable larval food plant for CG macro-moths. For example, larvae of the Small Elephant Hawkmoth *Deilephila porcellus* (L.) feed primarily on Lady's Bedstraw *Galium verum* (L.) (Waring & Townsend 2009). This plant was clearly present on all four CG patches, but was only sighted on 1 of 16 AES interventions.

I propose that CG species eclose almost exclusively on CG habitat, but that they will be attracted to use nectar and scarce larval host plants on AES interventions if they are easily reachable by dispersal. In other words, the AES interventions in this study might function as "sink habitat" for CG macro-moths (Watkinson & Sutherland 1995). If they do (and this remains to be tested), then adding more and more interventions could lead to diminishing returns. This would be because as nectar resources for adults increase, these AES interventions might fail to provide adequate larval resources for CG species, thus the total population size will be increasingly limited by survival from egg

to pupa. Even where eggs are laid on host plants in AES interventions, the success of offspring could be strongly reduced by spill-over of sprayed agro-chemicals (Hahn *et al.* 2015). In particularly severe cases AES interventions could represent an "ecological trap" for specialized species, whereby individuals waste time and energy in flight and reproduction with no net benefit to the population. Reducing agro-chemical spill-over on AES interventions might make "ecological trap" situations less likely to occur.

I have provided evidence of the value of general-purpose AESs for different groups of moths. This evidence can be used to interpret how these important nocturnal pollinators can benefit from habitat features created through AES. This information should be very useful for decision-makers, but it must be considered in relation to the goals of the AES. For example, declines in wider countryside moths are ongoing (Fox *et al.* 2014), and I do not address the fact that farmland that is isolated from SNH might be most in need of enhancements to ecosystem services such as pollination (Ricketts *et al.* 2008). There are also caveats when using the abundance of adult macro-moths to indicate population size or viability: my results do not ascertain that AES interventions benefit macro-moths at the larval stage. I propose that future work should (1) examine how connectivity to SNH affects the wildlife benefits of large-scale habitat creation that is tailored to priority species (2) consider which landscapes are most in need of the ecosystem services that habitat creation might provide and (3) survey all stages of the life-cycle of the taxon of interest.

2.6.Conclusions

I have found compelling evidence that macro-moth abundance on arable field margins can be increased through small-scale AES habitat creation (see also Fuentes-Montemayor, Goulson & Park 2011; Merckx *et al.* 2012). Furthermore, if adequate geographical and ecological data are available, spatial targeting advice can improve the outcomes of AES habitat creation. For example, if land managers aim to benefit priority species using generic AES interventions, I propose a strategy of clustering interventions around those species' core habitat. Nevertheless, when targeting habitat creation relative to SNH, the mechanisms through which species are expected to benefit from created

habitat must be considered. I hope this work will lay the foundation for similar empirical studies based on different taxonomic groups; this would facilitate the production of a set of generic targeting guidelines that could be applied *a priori* based on species' ecological traits.

Chapter 3: Successful restoration of moth abundance and species richness in grassland created under agri-environment schemes

A version of this chapter was published in 2017 in the journal *Biological Conservation* (Alison *et al.* 2017). Jamie Alison and Jenny Hodgson designed the study with help and feedback from Simon Duffield, Mike Morecroft and Rob Marrs. Jamie Alison and Simon Duffield secured permission for moth surveys across Hampshire, Wiltshire and Berkshire. Simon Duffield and Mike Morecroft helped with wildflower surveys. Jamie Alison conducted the field work and data analysis and wrote the manuscript. Simon Duffield, Mike Morecroft, Rob Marrs and Jenny Hodgson provided feedback on the manuscript.

3.1.Abstract

Restoring intensive agricultural fields to species-rich semi-natural grassland could have profound effects on biodiversity and ecosystem services. However, only a minority of European agri-environment scheme funding is currently devoted to such measures (<1% in the UK) and too few studies compare biodiversity on restored habitats with that on appropriate control and reference sites. As a result, there is a lack of advice for land managers on how to implement habitat restoration to maximise conservation outcomes, especially for insects. I present a landscape-scale field study in which I tested whether the abundance and species-occurrence of moths (Lepidoptera) differed between arable fields, fields restored to species-rich grassland, and semi-natural calcareous grassland (CG). I also tested whether moths were affected by the frequency of CG indicator wildflowers, age of restoration and habitat connectivity of restored grassland. I found that the abundance of CG-associated moths on restored grassland was almost eight times that on arable fields, and abundance and species-occurrence did not differ significantly from that on semi-natural CG. The only group of moths that was more abundant on CG than restored grassland was associated with late successional stage habitats (e.g. woodland), which shows that trees and shrubs are key features maintaining insect biodiversity on CG. CG moths were more abundant on restored grassland sites where CG indicator wildflowers had established, suggesting that active enhancement of the plant community can increase the abundance of target insect groups. Restoring arable fields to species-rich grassland benefits moths over short timescales (as little as 3 years) and at great distances from semi-natural CG (up to 7km). It should play a pivotal role in future agri-environment schemes aiming to increase insect biodiversity.

3.2.Introduction

Agricultural intensification has been a major driver of biodiversity declines in landscapes worldwide (Balmford, Green & Phalan 2012) and has been linked to a decline in ecosystem services such as pest control and crop pollination (Landis, Wratten & Gurr 2000; Kremen, Williams & Thorp 2002). Areas that are rich in wildlife can provide ecosystem services on surrounding farmland (Albrecht *et al.* 2007), so protecting those areas is part of the solution. Studies in the UK show that 55% of species of conservation concern are largely restricted to protected areas (Jackson & Gaston 2008) , while insect species are more abundant in protected areas than elsewhere (Gillingham *et al.* 2014). However, in many regions preservation alone will not be sufficient to meet international targets on biodiversity (James, Gaston & Balmford 1999). For instance, parties to the Convention on Biological Biodiversity have committed to restoring at least 15% of degraded ecosystems before 2020 (CoP 1992), and this implies large-scale habitat restoration.

Habitat creation and habitat restoration have been key drivers of biodiversity increase in the UK and elsewhere (Albrecht *et al.* 2010; Hayhow *et al.* 2016). Benefits to wildlife can be variable depending on local and landscape factors (Woodcock *et al.* 2015), but an understanding of this variation can be used to maximise biodiversity increases from habitat restoration in future. For example, during the restoration of species-rich grassland, target assemblages of phytophagous beetles are more likely to be achieved if target plant communities are also present (Woodcock *et al.* 2010). This suggests that both plants and invertebrates can benefit from practical measures that enhance the floral community, such as spreading green hay as a seed source from nearby semi-natural grassland. Similarly, Alison *et al.* (2016) found that creating grass margins on arable fields only increases calcareous grassland moth abundance when there is a core patch of calcareous grassland habitat nearby. This reveals that spatial targeting has potential to increase the benefits provided by grass margins.

Habitat restoration across Europe largely depends on public investment through agri-environment scheme (AES) payments. For example, between 1998 and 2008 land

managers in England were compensated £280 (approx. €330/$360) per hectare per year to restore 2,373ha of arable land to species-rich grassland (<1% of AES funds paid to farmers over that period, NE 2009, NE 2013). To justify such costs and inform the allocation of AES funds in future, biodiversity on restored sites must be compared with that on (1) sites before habitat restoration (control sites, e.g. conventional farms in studies of AES interventions; Kleijn et al. 2006) and (2) sites that represent benchmarks for biodiversity (reference sites, e.g. existing semi-natural calcareous grassland; Woodcock et al. 2010). While previous studies have measured restoration success based on compositional similarity between communities on restored habitats and reference sites (Mitchell *et al.* 1999; Fagan *et al.* 2008; Woodcock *et al.* 2010, 2015), it is also important to consider the outcome where biodiversity is higher on restored habitats than on reference sites.

I present the first study to assess how restoring arable fields to grassland affects the abundance and species-occurrence (i.e. species richness) of moths (Lepidoptera) against the benchmark of existing semi-natural grassland. Moths are an appropriate study taxon because they are highly diverse, have known habitat associations and have experienced declines in the UK (Fox *et al.* 2014). These declines have been linked to agricultural expansion and intensification, for example Merckx et al. (2012) found a lower abundance of nationally declining macro-moth species where there was higher arable land cover within a 0.8km radius. Though the ecosystem services provided by moths are poorly understood, there is growing evidence that they are major nocturnal pollinators: a recent study found that 23% of sampled moths carried pollen (Macgregor *et al.* 2017). Defoliation by caterpillars can profoundly affect nutrient cycling, increasing the proportion of nitrogen retained in soil organic matter (Lovett et al. 2002). Furthermore, moths and caterpillars are a critical food resource sustaining populations of various insectivorous animals of cultural or economic value (e.g. great tits *Parus major*, Perrins 1991).

I survey both macro-moth and micro-moth species in three distinct habitat specialism groups (calcareous grassland moths, grassland generalist moths and other

moths) on arable fields (control), former arable fields that have been restored to species-rich grassland (treatment), and semi-natural calcareous grassland (reference sites). Calcareous grassland (CG) is recognised as a priority habitat across much of Europe (CEU 1992). While it supports very high biodiversity of plants and insects, the number and size of CG patches has declined over the last century due to agricultural intensification and abandonment (Poschlod & WallisDeVries 2002). I test for effects of the extent of CG habitat in the surrounding landscape on moths throughout my investigation, and collect data on both the age and CG plant community of restored grassland.

My study is designed to address two key questions: (1) How do moth abundance and species-occurrence on restored grassland compare with that on arable fields and semi-natural CG? I predict that abundance and species-occurrence of CG moths will generally be lowest on arable fields, intermediate on restored grassland and highest on CG. (2) Among restored grassland sites, how are moth abundance and species-occurrence affected by the frequency of CG indicator wildflower species, age of restoration and the extent of CG habitat in the surrounding landscape? I predict that CG moth abundance and species-occurrence on restored grassland will increase with the age of restoration, connectivity to CG and frequency of CG indicator wildflowers. My predictions primarily apply to the CG-associated moth species group, but I anticipate that grassland generalist and other moths will show weaker effects in the same direction. In answering the key questions outlined above, I aim to produce advice for land managers to optimise the benefits of AES habitat restoration in terms of both ecosystem services and the conservation of priority insect groups.

3.3.Methods

3.3.1. Geographic datasets and habitat connectivity

Four polygon layers were used to shortlist study sites in ArcMap 10.1 (ESRI, Redlands, California): (1) restored grassland managed under the "Higher Level Stewardship" (HLS) agri-environment scheme as the option "restoration/creation of species-rich,

semi-natural grassland" (NE 2013, NE 2014b), (2) cover of CG habitat according to local data centres (HBIC 2014; TVERC 2015; WSBRC 2015), (3) cover of protected areas in the form of Sites of Special Scientific Interest (NE 2014b) and (4) underlying chalk (soft calcareous rock) geology in Hampshire, Wiltshire, Berkshire and the surrounding area (BGS 2013).

Polygons of CG habitat were used to derive a continuous surface of "connectivity" to CG across Hampshire, Wiltshire and Berkshire at 100m resolution. First, polygons were converted to a 100×100 m raster, with the value of each cell corresponding to the % cover of CG within it. For each cell I calculated a connectivity metric that combined information on the distances to all other cells and the area of CG within them. Specifically, I followed Hanski (1994) and used a negative exponential kernel, with a mean distance of 1km, weighted by habitat area (see Appendix A2 for more details). This particular connectivity metric has been an informative variable in previous studies of Lepidoptera in farmed landscapes (Alison *et al.* 2016).

3.3.2. Site selection

I selected 32 former arable fields deliberately restored to species-rich grassland across 22 farms in southern England. Sites were selected through GIS shortlisting as well as recommendations from farmers and farm advisers. The aim was to select grassland fields that had been restored more than three years ago, were on underlying chalk and represented a wide range of connectivity to existing high-quality CG habitat. I recorded the start year and method of establishment of each restored grassland field during scoping interviews with land managers. At the time of study restored grassland fields were all managed under HLS. However, restoration had commenced within the last 20 years under a variety of initiatives, including both AESs and set-aside. Restored grassland fields had been established using a variety of methods, such as natural regeneration or sowing of wildflowers (see Table A8 for individual site characteristics). All were cut or grazed at least once per year (NE 2013).

Each restored grassland (treatment site) was paired to a similarly-sized arable field nearby (control site). Treatment sites ranged from 2.6 – 37.5ha (mean 14.7) while control sites ranged from 2.2 – 49.3ha (mean 16.3). The mean distance between sites in a pair was 423m, and both sites were on the same farm in 28 of 32 pairs. For eight field pairs I also identified a reference semi-natural CG site nearby (mean 837m away from closest treatment/control field). Semi-natural CG sites were widely distributed across the study area (see Fig. A2 for a map of study sites).

3.3.3. Moth and plant surveys

Surveys of both macro-moths and micro-moths (detailed in Appendix A3) were carried out on 21 good-weather nights between June 11th and September 3rd 2015. On each survey night 4-9 sites were sampled using one 15w actinic Heath-style light trap per site (purchased from Anglian Lepidopterist Supplies https://www.angleps.com/). These sites comprised 2-4 treatment-control pairs and any corresponding reference sites. Traps were placed approximately 100m from the field's boundary (or as close to the field centre as possible if the field was <200m wide). This would help to ensure that recorded individuals were actually in the field before they were drawn to the trap, as Heath traps typically have attraction radii of 10-30m (Merckx & Slade 2014). All sites were surveyed twice (giving a total of 144 samples), with a minimum interval of one night between consecutive surveys at a given site (median of three, maximum of seven nights). A different combination of treatment-control pairs was surveyed on each good-weather night; this allowed mixed-effects models to correctly attribute random variance to the night of survey and the field of survey. Using such a random effects structure, it was not necessary to have a fully balanced design with 32 reference sites. However I could deploy up to 9 traps at a time, so more than 50% of survey nights did include at least one reference site.

Moth species were divided into three habitat specialism groups based on the "habitat" section of their descriptions in Waring and Townsend (macro-moths; 2009) or Sterling & Parsons (micro-moths; 2012). These specialism groups represented (1) species associated with CG habitat ("CG species"), (2) species associated with grassland

but not specifically calcareous grassland habitat ("grassland generalist species"), and (3) species not strongly associated with grassland ("other species", see Appendix A3 for classification criteria).

Surveys of CG indicator wildflowers were carried out during the same period as moth surveys. I defined CG indicator wildflowers according to the relevant list from Natural England's HLS Farm Environment Plan (NE 2010; see Appendix A5 for a list of CG indicator species). Natural England is the organisation responsible for monitoring biodiversity on protected habitats and AES restored habitats in England. As such, the CG indicator wildflower list used here is also used by practitioners to determine whether AES grassland has developed into "priority" semi-natural habitat. On each restored grassland field, ten 50cm×50cm quadrats were surveyed for the presence of wildflower species that are indicative of CG habitat (see Appendix A5 for further details).

3.3.4. Analysis of moth abundance

All statistical analyses were carried out in *R* 3.0.3 (R Core Team 2017). I treated the two traps placed on a given site as separate data points during my analysis, which allowed me to account for night specific variation in trapping conditions using random effects. Furthermore, for each of 144 traps I extracted counts of moth individuals belonging to each of the three specialism groups described above. This resulted in three counts per trap, corresponding to CG moths, grassland generalist moths and other moths (432 observations in total). These observations were used as the response variable in generalised linear mixed models (GLMMs) in the package *glmmADMB* (Skaug *et al.* 2015). Negative binomial error structures were used to model overdispersion in count data. To account for non-independence in the data caused by repeat samples of fields and temporal autocorrelation, random intercepts were included for survey field and survey date.

I used model selection based on Akaike's Information Criterion (AIC, Burnham & Anderson 2002) to test for effects of variables on moth counts. For each of my key questions, I specified a maximal model and fitted that model as well as all possible

models nested within it. If a top model emerged with ΔAIC of the next best model > 2, I took this as the clear best model. Following Richards (2008), I report all models with ΔAIC ≤ 6 except those with a higher AIC than any simpler nested version. However, if no clear best model emerged (ΔAIC next best ≤ 2) I used model averaging in the package *MuMIn* (Barton 2014) to produce a consensus model, taking a weighted average of parameters from component models using Akaike weights based on AIC.

To address question (1) moth counts on arable fields, restored grassland and semi-natural CG were used as the response variable in GLMMs with three variables as fixed effects: "species specialism", "habitat type" and "connectivity to CG". Species specialism was a factor with three levels corresponding to counts of CG species, grassland generalist species and other species from each trap. Habitat type was a factor with three levels corresponding to traps on arable fields, restored grassland and semi-natural CG. Connectivity to CG describes the extent of CG habitat around a trap (see *3.3.1. Geographic datasets and habitat connectivity* and Appendix A2 for explanation of this variable). This variable was cube-root transformed and centred on the mean prior to model fitting in order to improve model fit and reduce the influence of extreme values on model outputs. I suspected that the effects of habitat type and connectivity might differ between specialism groups. Furthermore, I suspected that the effects of connectivity might differ between habitat types. As such I allowed all possible two-way interaction terms. The maximal fixed effects structure for question (1) was *moth counts ~ species specialism * habitat type + species specialism * connectivity to CG + habitat type * connectivity to CG.*

To address question (2) I only included moth counts on restored grassland as the response variable in GLMMs with four variables as fixed effects: "species specialism", "connectivity to CG" (defined as above), "CG flowers" and "age". In order to maximise my ability to discriminate restored grassland sites on the basis of their plant community, I chose to summarise the frequency of multiple CG-associated flower species with a single principal components analysis (PCA) axis. This axis (henceforth "CG flowers") is the negative of the first principal component, which captured 37.3% of the variation in

CG wildflower community composition across the 32 restored grassland fields. This variable was positively associated with the species richness of CG flowers (Fig. A3) and the frequencies of almost all CG flower species (Fig. A4). The raw species richness of CG flowers could have been used as a predictor, but I anticipated that the relative frequency of those species would also be important. My variable accounts for both frequency and species richness of CG flowers, thus I consider it to be more discriminating than CG flower species richness alone. "Age" is simply used to refer to the number of years since a restored grassland field was last under arable management, as determined during scoping interviews with land managers. I predicted that the effects of age, connectivity and CG flowers would be most positive for CG species, so I allowed two-way interactions between species specialism and each other variable. The maximal fixed effects structure for question (2) was *moth counts ~ species specialism * connectivity to CG + species specialism * CG flowers + species specialism * age.*

Before fitting GLMMs, I ensured that there was no strong correlation between my predictor variables to avoid erroneous conclusions that might arise from indirect effects. Pairwise Pearson's correlation tests between variables were non-significant, and absolute values of Pearson's *r* did not exceed 0.4 (Fig. A5).

3.3.5. Analysis of moth species-occurrence

I tested whether variables affecting abundance similarly affected the occurrence of moth species in each specialism group, which is proportional to species richness. I produced a second set of GLMMs corresponding to questions (1) and (2) using the same fixed and random effect structures as GLMMs of moth abundance. For each of 144 traps, I determined the number of moth species recorded in each habitat specialism group. This number was then expressed as a proportion of the total number of species recorded from the relevant habitat specialism group across the entire study. This proportion, hereafter "species-occurrence" was treated as a binomial response variable in GLMMs (432 observations in total). Within a given specialism group, an increase in species-occurrence is analogous to an increase in species richness. While it would have been

valid to analyse species richness using other error structures, I preferred using binomial error structures to avoid truncating or transforming the response variable.

3.4.Results

I captured and identified 11,252 individual moths belonging to 244 species from 140 light trap samples (4 samples failed because of wind, disconnection or interference from livestock). 6.9% of individuals belonged to 28 species that were determined *a priori* to be associated with CG habitat, whilst 54.5% of individuals belonged to 46 species associated with other grassland habitat. The remaining 38.6% of individuals belonged to 170 species that were either associated with other habitats, such as woodland, or of no strong habitat association. During plant surveys 17 species of CG flowers were recorded across all 32 restored grassland fields. The number of CG flower species per field ranged from 0 to 11 with a median of 3.

1.1. Comparing restored grassland with arable fields and calcareous grassland

When analysing the difference in moth abundance between arable fields, restored grassland and semi-natural CG, a clear best model emerged with an interaction between habitat type and species specialism (ΔAIC next best = 3.26, Table 2, full model list in Table A9). Moth abundance was greater on restored grassland than on arable fields, and this difference was larger for more specialized subsets of moths: CG moths were 7.7 times more abundant on restored grassland, grassland moths were 3.4 times more abundant, and other moths were 1.6 times more abundant (Fig. 6). For both grassland moths and CG moths, abundance did not differ significantly between restored grassland and semi-natural CG. However, for other species abundance was 2.0 times greater on semi-natural CG than on restored grassland (Fig. 6). Binomial GLMMs revealed that the effects of grassland restoration on species-occurrence mirrored those for abundance (Table A10). Species-occurrence was greater on restored grassland than on arable fields for all species groups, while occurrence of grassland and CG moth species did not differ significantly between restored grassland and semi-natural CG. However, occurrence of other species was higher on CG than on restored grassland.

The best model also contained an interaction between connectivity to CG and specialism. This shows that connectivity to existing CG habitat in the landscape was a useful predictor of moth abundance, and the direction of this effect depended on the habitat specialism of the species group in question. The effect of connectivity to CG on abundance was more positive for moths associated with CG habitat than for moths associated with other habitat, and this was true across restored grassland fields, arable fields and semi-natural CG. Only one other model had a $\Delta AIC \leq 6$ and a lower AIC than any simpler nested version, and this model did not include connectivity to CG at all ($\Delta AIC = 3.26$, Table A9). Connectivity to CG was not a useful predictor of species-occurrence in binomial GLMMs (not included in best model, Table A10).

1.2. Comparing restored grassland based on wildflowers, age and connectivity

When analysing how the abundance of moths on restored grassland was affected by frequency of CG flowers, age and connectivity to CG, no clear best model emerged (Table 3). Model averaged predictions showed that the abundance of CG moths, but not grassland or other moths, was greater on restored grassland that had a high frequency of CG flowers (Fig. 7a, Table 3, Fig. A6). There was a negative but non-significant effect of age of restoration on moth abundance regardless of species specialism, and no clear effect of connectivity to CG (Table 3, Fig. A6). In binomial GLMMs, a clear best model emerged with no effect of CG flowers, age or connectivity to CG on the occurrence of moth species on restored grassland (Table A11). While CG flowers apparently increased the abundance of CG moths, I found no effect of CG flowers, age or connectivity on the occurrence of moth species in any of the three specialism groups.

Table 2. Summary of fixed effect parameters in the lowest AIC model predicting the abundance of moths (Log Likelihood = -1536.37, AIC = 3103.93, ΔAIC next best = 3.26, see Table A9 for model selection). This generalised linear mixed model (GLMM, negative binomial error) included an interaction between the variables habitat type (3 levels: arable field, restored grassland (base level), semi-natural CG) and species specialism (3 levels: CG species (base level), grassland species, other species) as well as an interaction between connectivity to CG and species specialism. Random intercepts were included for field of survey and date of survey. This model had a dispersion parameter $\alpha = 2.00$, indicating that data were highly overdispersed.

Species group	Parameter	Estimate	Std. error
Calcareous grassland (CG) species (associated with calcareous grassland)	Intercept (CG species on restored grassland at mean connectivity to CG)	1.848	0.195
	Arable field	-2.041	0.212
	Calcareous grassland	0.130	0.316
	Connectivity to CG	0.039	0.033
Grassland species (associated with grassland but not calcareous grassland)	Grassland species (on restored grassland at mean connectivity to CG)	2.052	0.154
	Arable field	0.805	0.241
	Calcareous grassland	-0.390	0.362
	Connectivity to CG	-0.016	0.032
Other species (not associated with grassland or calcareous grassland)	Other species (on restored grassland at mean connectivity to CG)	1.418	0.150
	Arable field	1.544	0.237
	Calcareous grassland	0.665	0.356
	Connectivity to CG	-0.085	0.031

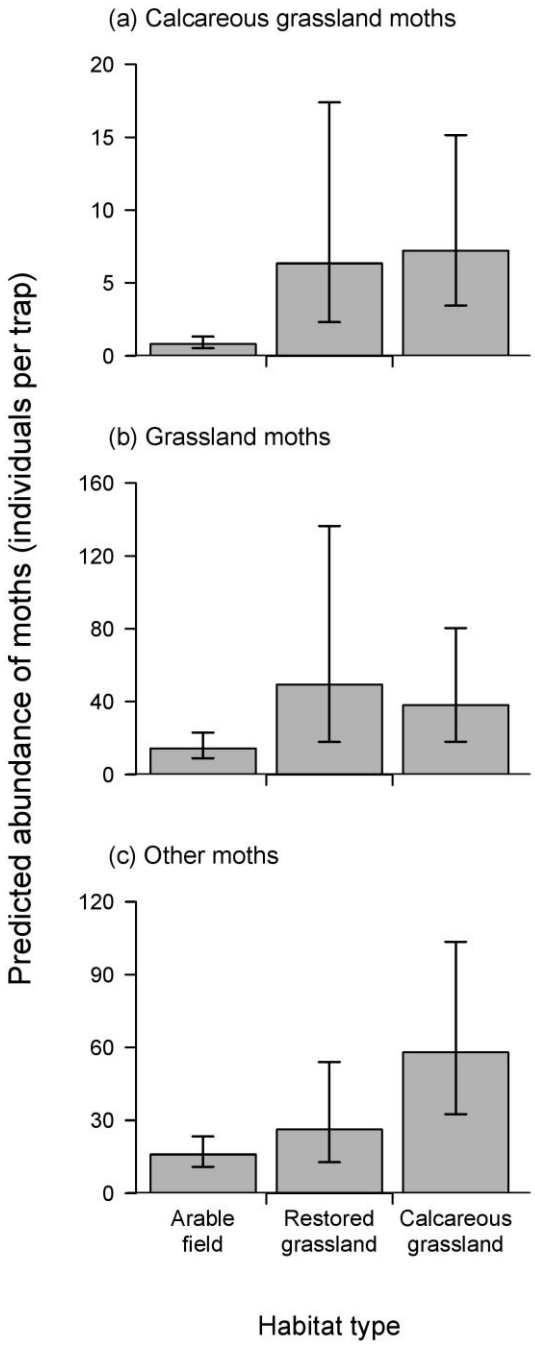


Figure 6. Predicted abundance (± 95% confidence intervals) of moths in three habitat specialism groups on three habitat types. Predictions were made for (a) calcareous grassland (CG) moths, (b) grassland moths and (c) moths not strongly associated with grassland (other moths). Habitat types considered were arable fields, fields restored to species-rich grassland, and semi-natural CG habitat. Predicted abundances and confidence intervals were calculated based on the generalised linear mixed model presented in Table 2 using the mean level of connectivity to CG of my study sites.

Table 3. Summary of generalised linear mixed models (GLMMs, negative binomial error) predicting the abundance of moths on arable fields restored to species-rich grassland. Fixed effects were allowed for "species specialism" (Spe), frequency of CG flowers (CGF), age of restoration (Age), and connectivity to semi-natural CG (Con). Random intercepts were included for field of survey and date of survey. Models were produced using the package *glmmADMB* (Skaug *et al.* 2015) and compiled for the table below using the package *MuMIn* (Barton 2014). Models are ranked in ascending order of AIC, with "+" indicating the inclusion of a variable in a given model. Following Richards (2008), I report models with $\Delta AIC \leq 6$; all of these models contained an interaction between CG flowers and habitat specialism, and this term consistently improved model parsimony irrespective of which other terms were included in the model (median $\Delta AIC = 7.63$, see Fig. A6 for details). The term for age (but not its interaction with specialism) improved model parsimony with some consistency, indicating a non-significant negative effect of age of restoration on moth abundance (median $\Delta AIC = 0.99$, Fig. A6). Including the term for connectivity to CG consistently decreased model parsimony (median $\Delta AIC = -2.16$, Fig. A6).

Rank	(Int)	Spe	CGF	Spe:CGF	Age	Spe:Age	Con	Spe:Con	Log-likelihood	AIC	ΔAIC
1	1.956	+	0.100	+	-0.011	+			-788.215	1602.203	0.000
2	2.274	+	0.097	+	-0.039				-790.492	1602.220	0.017
3	2.253	+	0.103	+	-0.038		0.042	+	-787.679	1603.438	1.235
4	1.810	+	0.099	+					-792.475	1603.956	1.753
5	2.255	+	0.098	+	-0.037		0.008		-790.451	1604.394	2.191
6	1.809	+	0.106	+			0.056	+	-789.312	1604.397	2.194
7	1.951	+	0.101	+	-0.011	+	0.004		-788.207	1604.494	2.291
8	1.919	+	0.106	+	-0.009	+	0.043	+	-786.106	1604.987	2.784
9	1.819	+	0.103	+			0.026		-792.074	1605.384	3.181

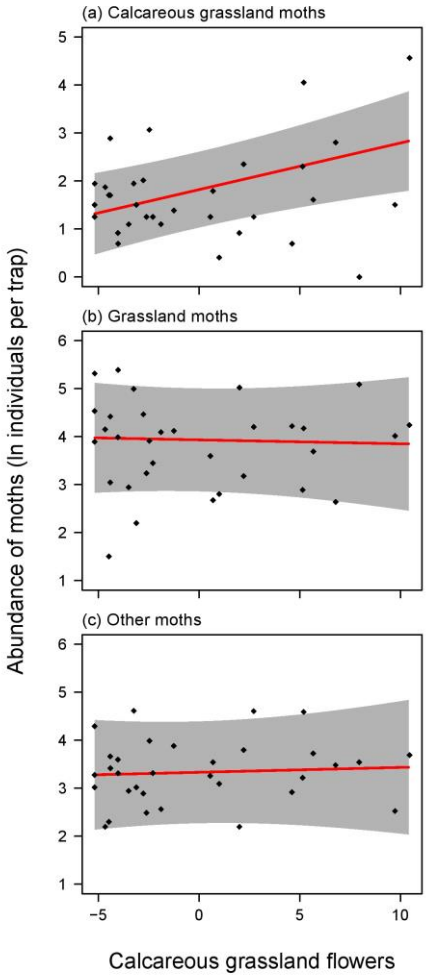


Figure 7. Model-averaged predictions (red lines) and 95% confidence intervals (CIs, grey area) of ln abundance of (a) calcareous grassland (CG) moths, (b) grassland moths and (c) moths not strongly associated with grassland (other moths) on restored grassland fields across a range of frequencies of CG indicator wildflowers. The variable "CG flowers" represents the negative of the first axis in a principle components analysis. It captured 37.3% of the variation in CG flower community composition across the 32 restored grassland fields, and was positively associated with the frequencies of almost all CG flower species (Fig. A4). Observed moth abundances (black diamonds) represent the ln mean moth abundance for each of 32 restored grassland fields across the nights on which they were surveyed. Predicted values and their standard errors were obtained by taking a weighted average, based on Akaike weights, of predictions from nine component models (Table 3). CIs represent predicted values ± 2s.e. (assuming a Gaussian sampling distribution for parameters) and are conditional on the random effects (uncertainty in random effects is not considered).

3.5.Discussion

3.5.1. Increases in moth abundance and species-occurrence following restoration

I found that the abundance and species-occurrence (i.e. species richness) of CG moths and grassland moths was not significantly different between restored grassland and semi-natural CG habitat. This result complements existing evidence to suggest that restoring arable fields to species-rich grassland can successfully restore the biodiversity of a variety of phytophagous insects (Woodcock *et al.* 2012a; b). I found that CG moths in particular were almost eight times more abundant on restored grassland than arable fields. Many types of AESs are considered unlikely to benefit uncommon species that are closely associated with traditional semi-natural habitat in agricultural landscapes (Kleijn et al. 2006; Ekroos et al. 2010). However, I add to a growing body of examples of AES interventions that do provide considerable benefits for rare or specialised species (Batáry *et al.* 2007; Merckx *et al.* 2010b; Pywell *et al.* 2012). Depending on the aims of the scheme in question, results such as these could help to prioritise AES interventions such as restoring arable fields to species-rich grassland which show promise for the conservation of specialised species.

In some regards my results are unexpected. For example, the similarity of the plant community between restored grassland and reference grassland tends to be low even after 60 years of restoration (Fagan *et al.* 2008). Indeed, on most of the restored sites in my study I found fewer than four CG indicator wildflower species, while a minimum of five is expected of priority CG habitat in lowland England (NE 2010). Nevertheless, larval host-plants and adult nectar are critical resources for Lepidoptera (Pywell *et al.* 2004b), so I suspect that the availability of such resources on restored grassland was approaching that on semi-natural CG. This is possible because some of the host-plants used by CG moths on restored grassland are not considered prime indicators of CG habitat. For instance, the hemiparasitic flower *Rhinanthus minor* (L.) was observed in 18 of 32 restored grassland fields and is the host-plant for the most abundant CG moth species in this study: the grass rivulet *Perizoma albulata* (D. & S., Waring & Townsend 2009).

Previous studies have reported less marked effects of grassland restoration on abundance and species richness of pollinating insects, which could be because they investigated less intensively-managed pre-restoration sites than I did (restoration from scrubland: Pöyry *et al.* 2004, 2005; Öckinger, Eriksson & Smith 2006; Maccherini *et al.* 2009; restoration from intensive grassland: Albrecht *et al.* 2010). By contrast, I studied restoration from an arable monoculture; the control fields in this study were mostly dedicated to wheat, oats and barley. I did not acquire details of pesticide application, but such management was a possibility on 26 of 32 arable fields that were not managed organically. One other study surveyed day-flying Lepidoptera on arable fields set aside to become grassland, revealing substantial increases in abundance and species richness during the first five years of restoration (Alanen *et al.* 2011), but no comparison was presented with nearby semi-natural grassland. In order to provide context for the state of biodiversity on restored grassland, it is important to evaluate semi-natural targets based on the same measures.

Interestingly, the only group of moths that was significantly more abundant on CG than on restored grassland was comprised of "other" species that are not strongly associated with grassland habitat. Some 148 of 170 (87%) of these species are associated with woodland, and trees and shrubs were absent from restored grassland but frequent on the CG sites I surveyed. Following this, I suspect many species of night-flying Lepidoptera respond positively to occasional woody vegetation on CG. This may also be true of day-flying Lepidoptera, e.g. Pöyry et al. (2005) identified a large subset of day-flying species which were more abundant in overgrown, abandoned grassland than in semi-natural or restored grassland in Finland. Historically, shrubs and trees have contributed to heterogeneity on CG habitats, thus promoting biodiversity (Benton, Vickery & Wilson 2003; Diacon-Bolli *et al.* 2012). Furthermore, Merckx et al. (2010a) have shown that hedgerow trees are an important source of shelter for moths in farmed landscapes. However, the grassland restoration investigated here does not promote the establishment of shrubs and trees, instead promoting scrub clearance (NE 2013). It is possible that such management choices have reduced biodiversity of some types of moths on restored grassland compared with nearby CG.

3.5.2. Effects of wildflower indicators, age of restoration and connectivity

The frequency of CG indicator wildflowers was positively associated with CG moth abundance on restored grassland, and this could be because they provided food for the larvae of some CG moth species. For example, *Galium verum* (L., observed in 10 of 32 restored grassland fields) is the primary host-plant for the small elephant hawkmoth *Deilephila porcellus* (L.). This CG moth species was observed in 8 traps on restored grassland, and five of those traps were on fields where *Galium verum* was confirmed to be present.

Nevertheless, there are two additional and compatible explanations for the effect of CG flowers observed here: The first is that CG flowers co-occurred with other host-plants for CG moths. For example, *Rhinanthus minor* is a key larval food plant which is not considered a CG indicator wildflower in this study, but it is known to facilitate the colonisation of CG indicator wildflowers during grassland restoration (Pywell *et al.* 2004a). The second compatible explanation is that some CG flowers, such as the legume *Lotus corniculatus* (L.), increased provision of nectar for adult moths. However, a wide variety of moth species feed on nectar as adults (Waring & Townsend 2009), so nectar provision might be expected to benefit all three specialism groups to a similar extent. In this study CG flowers only affected the abundance of CG moths, so I suspect that larval food plants were an important factor.

The effect of CG wildflowers reported here complements results from elsewhere that show greater restoration success for insects on restored grasslands that are florally diverse and/or similar to reference grasslands (Woodcock *et al.* 2010, 2015). While previous studies have measured restoration success based on community similarity to reference sites, in many cases biodiversity on those reference sites is already in decline (Diacon-Bolli *et al.* 2012). I instead compared restored and reference grasslands based on abundance and species-occurrence to show that absolute measures of biodiversity on restored grassland are high, especially when a community of indicator wildflowers has been established. However, my investigation was limited to habitat restoration at the scale of the entire field; future work could compare the cost-effectiveness of large- and

small-scale habitat restoration, and this would help to optimise allocation of AES funds between different scales of intervention.

Increases in the abundance and species-occurrence of moths that I observed on restored grassland probably occurred during the first few years of management. This is because restored grassland fields were 3-20 years old, and I found only non-significant decreases in moth abundance with age. This aligns with findings from previous studies on butterflies and moths which show that restoring arable fields to grassland can drastically increase abundance, species richness or community similarity to reference grassland within the first five years (Alanen *et al.* 2011; Woodcock *et al.* 2012a). However, it is possible that grassland restoration techniques have improved over time as the importance of plant community management has become apparent (Woodcock *et al.* 2010). If younger sites have been managed more appropriately, this could have masked any increase in moth biodiversity caused by age of restoration.

I found evidence that farmland that is well connected to semi-natural CG has an increased abundance of CG moths, confirming the role of semi-natural grasslands as population sources for a wide variety of insect groups (Öckinger & Smith 2007; Kohler *et al.* 2008; Woodcock *et al.* 2010, 2015; Fuentes-Montemayor, Goulson & Park 2011; Ekroos, Rundlöf & Smith 2013). However, the difference in overall moth abundance between restored and control sites did not change with connectivity to CG, and I did not find any significant effect of connectivity when analysing restored grassland alone. While Alison *et al.* (2016) used a similar study design and showed that grass margins on arable fields near semi-natural CG (<1km away) led to slight increases in CG moth abundance, here restored grassland supported high CG moth abundance even at great distances (0-7km) from semi-natural CG. These contrasting results might be explained by source-sink dynamics; grass margins might be "sink" habitat that is highly dependent on CG nearby to support populations of CG moths. A previous study suggested that uncultivated margins represented sink habitat for butterflies around semi-natural grassland (Öckinger & Smith 2007). Unlike grass margins, restored grassland fields might be large enough, or sufficiently resource-rich, that they contain self-sustaining

populations. Further mechanistic studies would help to fully understand how and where Lepidoptera populations depend on connectivity.

3.6.Conclusions

I show here that field-scale habitat restoration has a clear impact on the abundance of generalist and specialist insect species even over short timescales and at low connectivity to existing semi-natural grassland. Given that moths are major nocturnal pollinators (Macgregor *et al.* 2014) this could lead to an increase in ecosystem services on surrounding farmland. If practitioners aim to provide insect-mediated ecosystem services on nearby farmland, for example pest control and pollination (Landis, Wratten & Gurr 2000; Kremen, Williams & Thorp 2002), I propose that field-scale grassland restoration should play a pivotal role in future agri-environmental policies. In addition, I recommend management which allows for coverage of woody vegetation on restored grassland; occasional trees and shrubs are characteristic features of CG habitat and are important for the conservation of a wide variety of insect taxa (Diacon-Bolli *et al.* 2012).

Furthermore, practitioners may recognise specific habitats and their associated insect species as a priority (for example, CG in this study is considered priority habitat according to both national and EU level biodiversity policies). In this case I propose that land managers prioritise actions which increase the frequency of relevant plant species on restored grassland, for example spreading green hay from semi-natural grassland (Woodcock *et al.* 2010). My results show that this is also likely to increase the abundance of target insect groups that use those plants for nutrition and nectar, and that progress towards this goal can be rapidly assessed by monitoring easily identifiable wildflower indicators.

Chapter 4: An individual-based model to explore the interaction between agri-environment scheme-created habitats and source populations

Jamie Alison, Jenny Hodgson, Yevhen Suprunenko and Stephen Cornell designed the individual-based model. Jamie Alison ran simulations, analysed the results and wrote the manuscript. Jenny Hodgson, Stephen Cornell, Simon Duffield, Mike Morecroft and Rob Marrs provided feedback on the manuscript.

4.1.Abstract

Agri-environment schemes (AESs) have enormous potential to restore insect biodiversity and associated ecosystem services on farmland. However, empirical studies show that the benefit of an AES intervention, i.e. the increase in local abundance or species richness compared to a site without an intervention, depends on the surrounding landscape context. The cover of semi-natural habitat nearby is of particular relevance because it provides source populations of many insect species. In order to understand the mechanisms by which AES benefits are affected by distance to a source population, I designed an individual-based model. Adult and larval stages of 54 different hypothetical insect species were simulated in two-dimensional landscapes containing a linear source population and randomly distributed circular patches (AES interventions) with reproductive value equal to, or greater than, the surrounding matrix. Each hypothetical species had a unique combination of characteristics affecting whether they were generalist or specialist, and whether they moved more slowly when in patches (i.e. they were attracted to patches). I measured benefits of patches at a range of distances from the source population as in empirical studies, by comparing activity density of adults in patches to that in the matrix. I found that: (1) patch benefits declined with distance for all simulated species, although maximum benefits did not always occur adjacent to the source population; (2) the impact of spatial targeting, i.e. the increase in benefit of patches closer to the source population, was greatest for species which reproduced well in patches but not in the matrix, and which were attracted to patches; (3) spatial targeting appeared to increase patch benefits even if patches affected movement and not reproduction (i.e. patches were “ecological traps”) and (4) measuring relative benefits of AESs, as opposed to absolute benefits, led to contradictory conclusions about the impact of spatial targeting.

4.2.Introduction

Over recent decades the abundance and diversity of many species groups has declined in association with human activity (Butchart *et al.* 2010). Insects form a substantial proportion of the total biomass and species richness of ecosystems, and many carry out processes useful to humans such as pollination and decomposition (Kim 1993). As such, it is alarming that insect groups show strong evidence of declines where they have been sufficiently monitored (e.g. butterflies, bees, moths and carabid beetles in the UK: Thomas *et al.* 2004; Biesmeijer *et al.* 2006; Conrad *et al.* 2006; Brooks *et al.* 2012; butterlies and bees across wider Europe: Carvalheiro *et al.* 2013). The state of pollinators is of particular concern as it underpins the reproduction of the majority of wild plant species (Kearns, Inouye & Waser 1998). Furthermore, 35% of global food production relies on pollination to some extent (Klein *et al.* 2007; Potts *et al.* 2016). The causes of biodiversity declines are wide ranging, but it is clear that agricultural expansion and intensification have been key drivers (Balmford, Green & Phalan 2012; Hayhow *et al.* 2016).

Habitat restoration has been a key driver of local increases in biodiversity, and encouraging results have been recorded for insect groups across Europe (e.g. Maccherini *et al.* 2009; Alison *et al.* 2017). Agri-environment schemes (AESs) offer opportunities for habitat restoration, but also other interventions that increase biodiversity on farmland (e.g. organic farming, Hodgson *et al.* 2010). While AES interventions have had variable effects on wildlife depending on the region or species group considered (Kleijn et al. 2006), there is substantial evidence that they increase the abundance and diversity of various insect groups (e.g. butterflies: Rundlöf & Smith 2006; moths: Fuentes-Montemayor, Goulson & Park 2011; Merckx *et al.* 2012; bumble-bees: Pywell *et al.* 2012). As such, AES interventions benefit many insect species that are pollinators, and this could explain evidence from Switzerland and the UK that links AES interventions to increases in yield of pollinator-dependent crops nearby (Albrecht *et al.* 2007; Pywell *et al.* 2015).

AES interventions have the potential to increase biodiversity, but it may be possible to maximise benefits for wildlife through spatial targeting (placing AES interventions where they may have greater benefits for biodiversity, e.g. extensively farmed areas: Kleijn & Sutherland 2003; Whittingham 2007). Some AES interventions essentially create a new "patch" of habitat, so studies of reserve design and meta-population dynamics offer relevant advice as to where to place them. For example, a study by Diamond (1975) applied the principles of island biogeography to determine that a small patch will generally hold more species if it is placed closer to a large patch. Similarly, the occupancy of a habitat patch tends to increase with proximity to other large patches (Hanski 1994), while a landscape with a small number of large patches will have a higher meta-population capacity (which predicts population size) than a landscape with the same total area of habitat divided into many smaller patches (Ovaskainen 2002). However, agricultural landscapes do not always comprise a network of discrete patches in a hostile matrix (Baguette 2004); areas within them could instead be considered to fall on a continuum of habitat suitability. However, it has been shown that biodiversity decreases exponentially as continuous measures of land-use intensity increase (Kleijn *et al.* 2009). Thus, even without the simplifying assumptions of meta-population theory, the suggestion remains that biodiversity in AES interventions is higher where the surrounding landscape is more hospitable to wildlife (Kleijn & Sutherland 2003).

Understanding of the benefits of AES interventions is in some ways limited by the methods used to study them. Studies tend to evaluate the effects of AES interventions by collecting data from nearby equivalent sites without AES interventions (i.e. control sites, Kleijn & Sutherland 2003). The benefits of AES interventions are then generally calculated as abundance or species richness on treatment sites minus that on control sites (i.e. absolute benefit to biodiversity, Fig. 8a & b). These benefits may vary with landscape context in complex ways because they depend on biodiversity both before and after an AES intervention takes place. For example, Tscharntke *et al.* (2005) argued that interventions may be redundant if there is already high spill-over of species from semi-natural habitat onto intensively farmed land. As a result, AES interventions

might actually make a bigger difference in landscapes with intermediate coverage of semi-natural habitat than in the most biodiverse landscapes. This argument has gained support from international meta-analyses, which have shown reduced benefits of AES interventions for insect pollinators where coverage of nearby semi-natural habitat is greater than 20% (Batáry *et al.* 2011; Scheper *et al.* 2013). A further complication is that studies might calculate the benefits of AES interventions in relative terms rather than absolute terms. These two approaches can lead to contrasting conclusions about where in the landscape AES interventions will lead to the greatest increase in biodiversity (e.g. Fig. 8b & c).

Most studies of the landscape context of AES interventions have tended to focus on the intensity of farming, or the availability of semi-natural habitat in the wider landscape (Kleijn et al. 2011). The latter focus may be justified because semi-natural habitat provides source populations of a wide variety of insect species in agricultural landscapes (Öckinger & Smith 2007; Kohler et al. 2008; Ekroos, Rundlöf & Smith 2013). However, evidence suggests that the relationship between the benefits of AES interventions and distance to semi-natural habitat depends on the species group in question. For example, Alison et al. (2016) found that AES grass margins benefit grassland generalist moths throughout an agricultural landscape, but only benefit calcareous grassland moths when there is semi-natural calcareous grassland habitat nearby. Furthermore, the presence of source populations in semi-natural habitat may be less relevant for some types of AES intervention than others: A subsequent study by Alison et al. (2017) on similar groups of moths found no significant relationship between benefits of restored species-rich grassland and connectivity to existing calcareous grassland. The characteristics of a given species group and AES intervention appear to determine whether benefits increase, decrease or remain stable with distance from a source population. If the mechanisms behind this effect were properly understood, land managers could use knowledge of the ecology of a target species group to decide (1) whether spatial targeting of AES interventions is likely to make a difference, and (2) where in the landscape benefits of AES interventions are likely to be maximised.

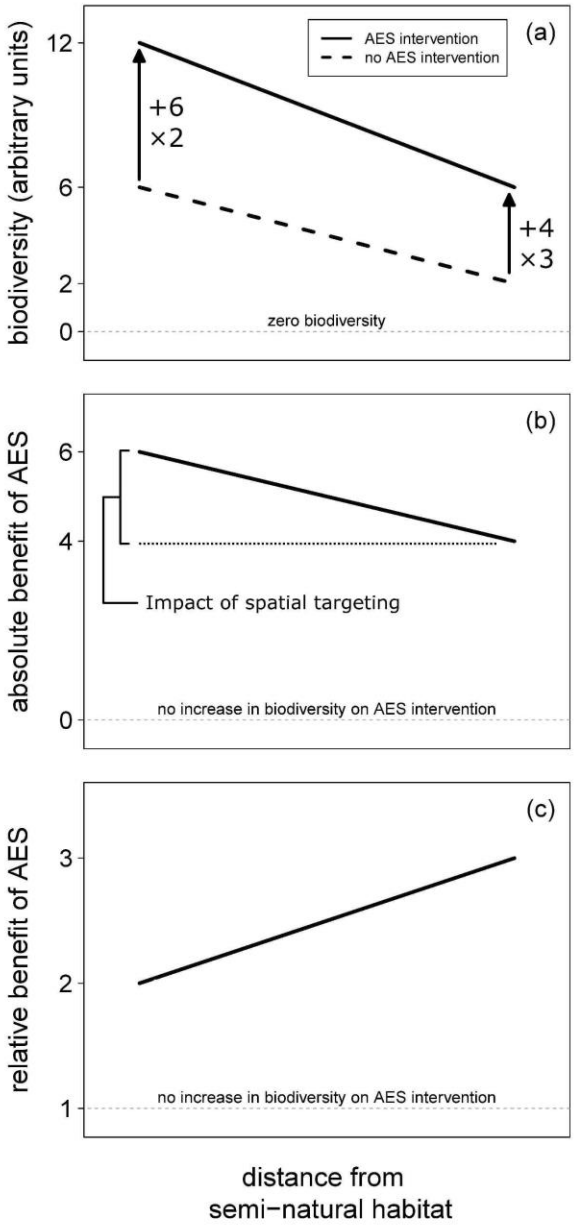


Figure 8. Hypothetical relationship between distance from semi-natural habitat and (a) biodiversity on sites with (solid line) and without (dashed line) agri-environment scheme (AES) interventions, (b) absolute benefit of AES interventions and (c) relative benefit of AES interventions. Absolute benefit is calculated as biodiversity on AES interventions minus that on control sites, i.e. the solid line minus the dashed line in panel (a). Relative benefit, on the other hand, is calculated as biodiversity on AES interventions divided by that on control sites. The impact of spatial targeting is represented throughout this chapter as the difference between the maximum and the minimum absolute benefit across the full range of distance to the source population (i.e. semi-natural habitat).

Nonetheless, benefits of AES interventions are often deduced from observations of insect species at the adult life stage. As such, apparent benefits could reflect individual movement and foraging choices rather than local population dynamics. In some cases AES interventions could even represent "ecological traps" that have the effect of attracting individuals without providing any benefits to survival or reproduction (Battin 2004). This has been identified as a potential caveat to advice offered by studies of spatial targeting of AES interventions (Alison *et al.* 2016). However, it is unclear how the effect of the landscape context on AES benefits might vary between ecological traps and habitats with improved survival or reproduction.

I designed an individual-based model to test how the benefits of created (AES) patches depend on distance to a source population across 54 different hypothetical insect species. Each hypothetical species interacted with the landscape in a different way, and was characterised by a unique combination of four parameters: the proportion of the landscape that comprises patches of high reproductive value, the egg-laying rate in those patches, the egg-laying rate in the surrounding matrix and the mean step length inside patches. The proportion of the landscape that comprises patches, egg-laying rate in patches and egg-laying rate in the matrix all determine how widespread, abundant and generalist a species is. A lower mean step length in patches represents attraction, as individuals that encounter patches take shorter steps, and spend more time, within them. The mean step length parameter allowed me to simulate the scenario where patches affect species' movement but not their reproduction. My model also included a number of other parameters, underpinning processes such as density-independent death and density-dependent death, but these were fixed across all species.

For each species I calculated the benefits of patches by comparing the density of adults to that in the matrix, in the same way that empirical studies have compared biodiversity on AES interventions to that on control sites. I quantified benefits by firstly taking density in patches minus density in the matrix (absolute benefits), and secondly dividing density in patches by density in the matrix (relative benefits). I looked at how the benefits of patches for the 54 hypothetical species varied with distance from a large

source population (representing semi-natural habitat), addressing the following key questions: (1) how do the characteristics of a species affect the distance from the source population at which patches have the greatest benefits? (2) for which types of species will distance to the source population make the biggest difference to the benefits of patches, i.e. for which species is the impact of spatial targeting the highest? See Fig. 8b & c for an explanation of the impact of spatial targeting. I aim to understand the mechanisms behind the results of empirical studies of AES interventions, while also providing rules of thumb to aid land managers in charge of spatial targeting.

4.3.Methods

4.3.1. Model overview

I implement spatially-explicit individual-based simulations using the C-program *ppsimulator* (Cornell *et al.* 2017). My model is designed to simulate the population dynamics of annual insect pollinator species with discrete, non-overlapping larval and adult stages. Simulations take place in a two-dimensional 10 × 10 km torus space, and landscapes comprise an agricultural matrix of relatively low reproductive value containing randomly-placed patches of a higher reproductive value (representing AES interventions). These patches are circular and 50m in diameter. I represent a semi-natural habitat "source population", without simulating all its internal dynamics, by adding a large number of adult insects each year at the origin on the first dimension (the x-axis) and at random on the second dimension (the y-axis). The distance from the source population affects the "spill-over" received by patches and the matrix, and the influence of immigrant individuals on local population dynamics. Thus, distance from the source population can be considered a proxy for the availability of semi-natural habitat (however that availability may arise in practice). The desired output of the model is a measure of the increase in density of individuals in patches compared with the matrix across a range of distances from the source population.

Entities in simulations are defined by two state-variables: class and location. Class details whether an entity is (1) an adult in the matrix, (2) an adult in a patch, (3) a

patch or (4) an egg/larva (Fig. 9). Location details the x- and y-coordinates of an entity at a given point in simulation time. The model is made up of two stages: the adult stage, hereafter "summer", and the larval stage, hereafter "winter". These two stages are run iteratively, with the output of one stage forming the input for the other. A "year" in the model is defined as a single instance of summer followed by winter, and each simulation was run for 30 years to approximate equilibrium dynamics.

Adults and eggs/larvae undergo different processes during the two model stages: During summer, adults move through the landscape at random, produce eggs/larvae and undergo density-independent death. Adults also change class based on whether they are in patches or in the matrix, and this can affect the rate at which they lay eggs or their mean step length (through class-specific model parameters, see below). During winter, eggs/larvae undergo density-dependent death as if competing for local resources. *ppsimulator* schedules processes using the Gillespie algorithm (Gillespie 1977) based on the user-specified rates of each process per unit of simulation time. For the summer stage of the model, I specify rates such that the unit of time is days; this allows me to use empirical data on insect dispersal and lifespan to derive realistic model parameters. For the winter stage of the model the unit of time is arbitrary, as only the final outcome of density dependent survival matters for subsequent dynamics.

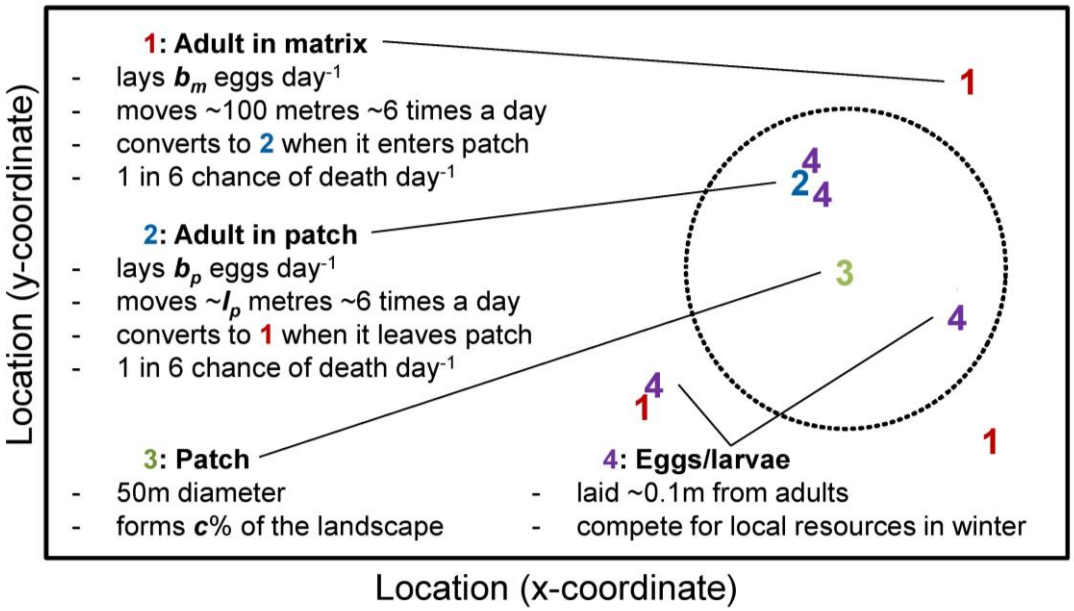


Figure 9. A hypothetical snapshot of a small area of simulation space, containing the four classes of simulated entities: adults in the matrix (1, red), adults in a patch (2, blue), patches (3, green) and eggs/larvae (4, purple). Information about the processes that the entities experience are outlined with reference to the variable parameters c, b_p, b_m and l_p; see Table 4 for more details. At the beginning of each simulated year adults are distributed as the source population (see Methods: *Overview* for details) and the eggs/larvae that survived the previous winter. The random distribution of patches is determined before the start of each simulation and is fixed across the 30 years.

4.3.2. Model parameters

I ran simulations of 54 hypothetical species. Each species was represented by a unique combination of values of four variable parameters (c, b_p, b_m and l_p; Table 4). These parameters can be interpreted as characteristics of a species that affect how it interacts with a patchy landscape. For example, c represents the proportion of the landscape that comprises patches of relatively high reproductive value for a species. In a single real-life agricultural landscape, this value might be very small for a specialised species but large for a habitat generalist. Across hypothetical species I varied the coverage of patches, c; the egg-laying rate (or birth rate) in patches, b_p; the egg-laying rate in the matrix, b_m and mean step length in patches, l_p. Patches were meant to represent refuges for insects in a more hostile matrix, so the value of b_p was always equal to or higher than the value of b_m. Furthermore, the value of l_p was always equal to or lower than the value of l_m because empirical studies of the movements of insects often show greater displacement in less-favoured habitats (Schultz 1998; Schultz & Crone 2001; Ovaskainen *et al.* 2008).

I set all parameters in my model to values considered biologically realistic for insects of the order Lepidoptera. While the design of my model should be relevant to a wide variety of other insect pollinators, there is a comparatively rich literature on Lepidoptera; many studies even collect data specifically to parameterize individual-based models (Brown & Crone 2016). Most parameters in the model were fixed, but four key parameters were allowed to take a finite range of values (Table 4). Justifications for upper and lower bounds of variable parameters are outlined below, while values and justifications for fixed parameters are outlined in Table 5.

Table 4. Values used for the four parameters that were varied across simulations. Each of the 54 possible combinations of these parameters characterises a hypothetical species. These parameters apply to the summer stage of the model, meaning that they affect how adults, not larvae, interact with the landscape. *c* stands for coverage of patches, *b* stands for birth rate in patches or the matrix and *l* stands for length of steps in patches. Justification of these parameter ranges is provided in the methods.

Parameter	Description (units)	Low value	Medium value	High value
C	Coverage of patches in the landscape for a given species (%)	2	4	8
b_p	Egg-laying rate of adults in patches (eggs d^{-1})	0.12	1.00	4.00
b_m	Egg-laying rate of adults in matrix (eggs d^{-1})	0.00	0.06	0.12
l_p	Mean step length in patches (m)	20	-	100

Table 5. Values used for parameters that were fixed across simulations. Values were chosen based on both expert opinion and empirical studies of the life-history of Lepidoptera. Brief justifications are provided.

Stage	Parameter	Description	Value	Justification
Summer	$B_p = B_m$	Standard deviation of the Gaussian kernel of the distribution of eggs around a laying adult in a patch (B_p) or in the matrix (B_m).	0.1 m	Selected so that eggs are laid in a small area around the adult.
	$d_p = d_m$	Density-independent death rate of adults in patches (d_p) or in the matrix (d_m).	0.166 d^{-1}	Selected to give a mean lifespan of 6 days. One study assembled mean lifespans of 24 species of Lepidoptera, giving a range of 4.4 to 25.5 days (Jervis, Ferns & Boggs 2007), while many other studies report values at the lower end of this range. I chose 6 days in consideration of the fact that simulated adults would lay eggs throughout their lives, whereas real-world adults have some pre- and post-reproductive lifespan (Leather, Watt & Barbour 1985).
	$s_p = s_m$	Step rate of adults in patches (s_p) or in the matrix (s_m).	6 d^{-1}	These parameters affect the number of different locations at which adults lay eggs on a given day. An intensive observational study by Wiklund (1977) found that eggs were laid in up to 23 locations per day. I chose 6 steps per day for simplicity and considering that most eggs never become adults (see below explanation of egg-laying rate).
	l_m	Mean step length of adults in the matrix.	100 m	Given s_p and s_m, this parameter (as well as the variable parameter l_p, Table 4) affects the mean daily displacement of individuals. A recent study on macro-moths collected mark-release recapture data for 41 species (Slade *et al.* 2013). Mean predicted weekly displacement of these species across a

				combination of habitat patches and the matrix was ~235m. A study of the butterfly *Parnassius mnemosyne* found mean daily displacement in the matrix of ~275m (Ovaskainen *et al.* 2008). The latter study provided a measure of displacement through the matrix specifically, thus I chose 100m corresponding to mean daily displacement of 245m per day.
	$t_p = t_m$	Rates of class transformation of adults.*	V. high	Set to be very high so that classes of adults are updated based on location as quickly as possible given computational restraints.
Winter	K	Rate of density-dependent death of larvae.	40	This parameter was fixed at an arbitrary value of $k = 40$. Then, the duration of winter was adjusted to 3.54, which meant that if the landscape was homogenous and the egg-laying rate was 4 eggs d^{-1}, the carrying capacity would be ~100 individuals ha^{-1}. A study has estimated density of several moth species assuming 1:1 sex ratio, and values ranged from 20 to 2000 individuals ha^{-1} (Nieminen 1996).
	K	Standard deviation of the Gaussian kernel for density-dependent death of larvae.	5m	A relatively short distance was chosen; an infestation experiment on a pest species of Lepidoptera finds that ~50% of recovered larvae don't leave their natal plant (Ostlie & Ross 1990).

***** These parameters ensure that adults can undergo different processes based on their spatial location. Adults in patches transform into adults in the matrix at rate t_m when outside a patch (but still within 200m of it; this restriction is necessary for computational efficiency). Adults in the matrix transform into adults in patches at rate t_p when inside a patch. The transformation from adults in patches to adults in the matrix, and vice versa, was imperfect (see Appendix A6 for further explanation).

I used a lower bound of c = 2% to represent species with realistic but low coverage of reproductive habitat in intensive agricultural landscapes. For example, some species might only reproduce on grass margins or sown flower strips on farmland and such habitat represents >1% of arable land in Hampshire, UK (Alison *et al.* 2016). On the other hand, an upper bound of c = 8% might represent a species which can reproduce on any arable margin, regardless of wildlife-friendly management. I used a lower bound of b_p = 0.12 eggs d^{-1} in patches because in preliminary simulations where the landscape was 100% patch-quality, species would just about go extinct without a source population (i.e. patches are definitely 'sink' habitat, Pulliam 1998). I used an upper bound of b_p = 4.00 eggs d^{-1} even though egg-laying rates in the literature can be upward of 20 eggs d^{-1} (Wiklund 1977; Leather, Watt & Barbour 1985). This was because there is no density-independent death of eggs/larvae in my model; eggs/larvae laid in isolation would always survive to adulthood. I opted for a reduced upper bound to incorporate the density-independent death that occurs in eggs/larvae of real Lepidoptera, which might be upward of 50% (Tammaru, Kaitaniemi & Ruohomaki 1995). I then used $0.00 \leq b_m \leq 0.12$ to cover the full possible range of "sink" habitat egg-laying rates which did not exceed egg-laying rates in patches. Finally, I allowed l_p to drop from 100m to 20m, which combines with s_p (Table 5) to give a mean daily displacement of ~50m. Studies have tended to find higher daily displacement of Lepidoptera in habitat patches (Schultz 1998; Ovaskainen *et al.* 2008). However, the patches considered in those studies were larger than the patches in my simulations, so using a greater step length in patches may have led to unrealistically low residence times.

4.3.3. Model initialisation

I ran 30 simulations with different random number seeds and different random arrangements of patches for each of the 54 hypothetical species. Year one of each simulation started with summer, and 10 adults ha^{-1} were distributed at random throughout the landscape. For each subsequent summer, I added a large number of immigrants to the landscape at the origin on the first dimension and at random on the second dimension ($x = 0$, $y \sim U[0,1]$). This approximated immigration from a source population in a large strip of semi-natural habitat. The number of immigrants to add was

determined using preliminary simulations of dispersal from an area of high population density; for a single summer in a 10km × 10km landscape, a 2km × 10km strip of 100 adults ha^{-1} was allowed to disperse into the surrounding homogenous matrix. After all individuals died, ~111,000 individual days had been spent in the matrix. Dividing this value by the average lifespan (6 days) showed that this immigration was equivalent to 18,500 individual adults. Approximating immigration from a source population, rather than explicitly simulating it, drastically improved computational efficiency of simulations. However, if the source population had been simulated explicitly, initial adult densities would probably be lower at the boundary with the agricultural matrix than toward the centre of the source population. My approximation of the source population does not account for such edge effects.

4.3.4. Data analysis

In years 26-30 of each simulation, I recorded the location of all adults at the start of each summer and then at daily intervals until the end of summer (either when all adults died or after 100 days had passed). These data were aggregated to activity densities of adults in patches and adults in the matrix within each interval of 100m from the source population (e.g. 100-200m is one distance category). For each distance category in each random seed replicate, I took the total count of adults in patches or the matrix across all days in all five years. I then divided these counts by the area of the relevant land-use type and the number of years, giving a measure of activity density (adult days ha^{-1} y^{-1}). Finally, I calculated the means of these activity densities across the 30 random seed replicates.

I characterised the shape of the relationship between activity density A and distance from the source population d using asymptotic-exponential functions (Eq. 1 & 2). Separate relationships were fitted for patches and the matrix using the *nls* function in *R* 3.4.0 (R Core Team 2017). Least-squares estimates were obtained for the power of distance i, the Y-intercept b and the natural logarithm of the rate constant c. However, I fixed the asymptote a because areas very far from the source population should have demonstrated population dynamics as if there was no source population at all. The value

for the fixed asymptote was thus determined by running a parallel set of simulations that was identical to the set described above, except that a source population was not included. From these simulations I calculated activity density of adults in patches and in the matrix during years 26-30 for each of the 54 species. For each species, I took a_p as the mean activity density in patches, and a_m as the mean activity density in the matrix, across 30 random seed replicates.

$$A_p = a_p + \left(b_p - a_p\right)e^{-e^{c_p} d^{i_p}} \quad \textbf{Equation 1}$$

$$A_m = a_m + (b_m - a_m)e^{-e^{c_m} d^{i_m}} \quad \textbf{Equation 2}$$

I did not test the fit of different functional forms to activity density in patches and in the matrix. This was because asymptotic-exponential functions fitted the observed data well (Fig. 11a-d), and were suitable for determining the impact of spatial targeting as described below.

For each distance category the absolute benefit of patches was taken as activity density of adults in patches minus activity density in the matrix (as predicted by the fitted lines). Correspondingly, the relative benefit was taken by dividing activity density in patches by activity density in the matrix. I also calculated the increase in absolute benefit of patches that might be achieved through spatial targeting (henceforth impact of spatial targeting, Fig. 8b). This represents the difference between the maximum achievable benefit of a patch (at the optimal distance from the source population) and the minimum benefit of a patch (at the least beneficial distance). In this study, whenever the effect of distance on the benefit of patches was non-negligible, benefits were greatest adjacent to the source population and smallest at high distance (Fig. 11). As such, the impact of spatial targeting for a given species was always calculated as the benefit of patches adjacent to the source population minus the benefit of patches infinitely far away, i.e. (b_p - b_m) - (a_p - a_m).

4.4.Results

Mean activity density across the entire landscape for the 54 hypothetical species ranged from 12.51 to 92.25 individual days ha^{-1} $year^{-1}$, increasing with egg-laying rate in patches b_p and the matrix b_m (Fig. 10). When $b_p > b_m$, density also increased with the coverage of habitat patches c. Decreasing the step length of adults in patches l_p almost always led to an increase in mean activity density, as adults spent a longer proportion of their lives in patches thus they laid more eggs (Fig. 10). Exceptions to this occurred when (1) $b_p = b_m$ or (2) b_p, b_m and c were all set to their highest values (here, the increase in eggs laid in patches was probably offset by density-dependent death in patches and decreased egg-laying in the matrix).

4.4.1. Effects of distance from source population on patch benefits

Activity density in both patches and the matrix always declined with distance from the source population (Fig. 11a-d). The source population supplements the nearby areas of the landscape with individuals, but becomes less relevant as distance increases; areas that are very far away behave as if there were no source population at all. When there is no source population, some species are bound for extinction (Fig. 11a) while others simply survive at lower densities than if there were a source population (Fig. 11b-d).

I calculated the absolute benefit of patches compared to the matrix, which was the activity density of adults in patches minus activity density in the matrix (lighter lines minus darker lines in Fig. 11a-d). For all hypothetical species, the absolute benefit of patches was lowest at the greatest distance from the source population (Fig. 11e). For species that were bound to extinction when there was no source population, absolute benefits also declined towards zero with distance from the source population. This reflects how the source population was critical for the colonisation of patches (Fig. 11e, red lines). For these species the maximum absolute benefit was consistently observed at the shortest recorded distance from the source population. For other species, absolute benefits declined to some positive asymptote, so patches benefited the activity density even at great distance from the source population (Fig. 11e, blue, yellow and green

lines). For some such species, maximum absolute benefit occurred somewhere beyond the shortest distance from the source population, but the maximum benefit was always within 500 m, and was never substantially higher than the benefit within 100 m (Fig. 11e, yellow and green lines).

If patches affected dispersal and not reproduction of a species, maximum absolute benefit of patches still occurred as close as possible to the source population. Some hypothetical species had the same egg-laying rate in both patches and the matrix (i.e. $b_p = b_m = 0.12$), but had a lower step length in patches. Even though egg-laying rate was not increased in patches, density of adults was higher in patches than in the matrix for these species. Furthermore, the absolute benefit of patches for these species was greatest adjacent to the source population (Fig. 12b), an effect which mirrored that seen when patches affected reproduction and not dispersal (Fig. 12a).

As well as absolute benefit, I calculated the relative benefit of patches compared to the matrix. This was the activity density of adults in patches divided by activity density in the matrix (lighter lines as a proportion of darker lines in Fig. 11a-d). While the absolute benefit of patches decreased with distance from the source population (Fig. 11e), relative benefits increased with distance (Fig. 11f). The only exceptions occurred when $b_p = b_m$; here the relative benefit of patches remained constant as distance increased. Thus, the method used to quantify the benefit of patches compared with the matrix strongly affects the distance at which benefits are seen to be maximised.

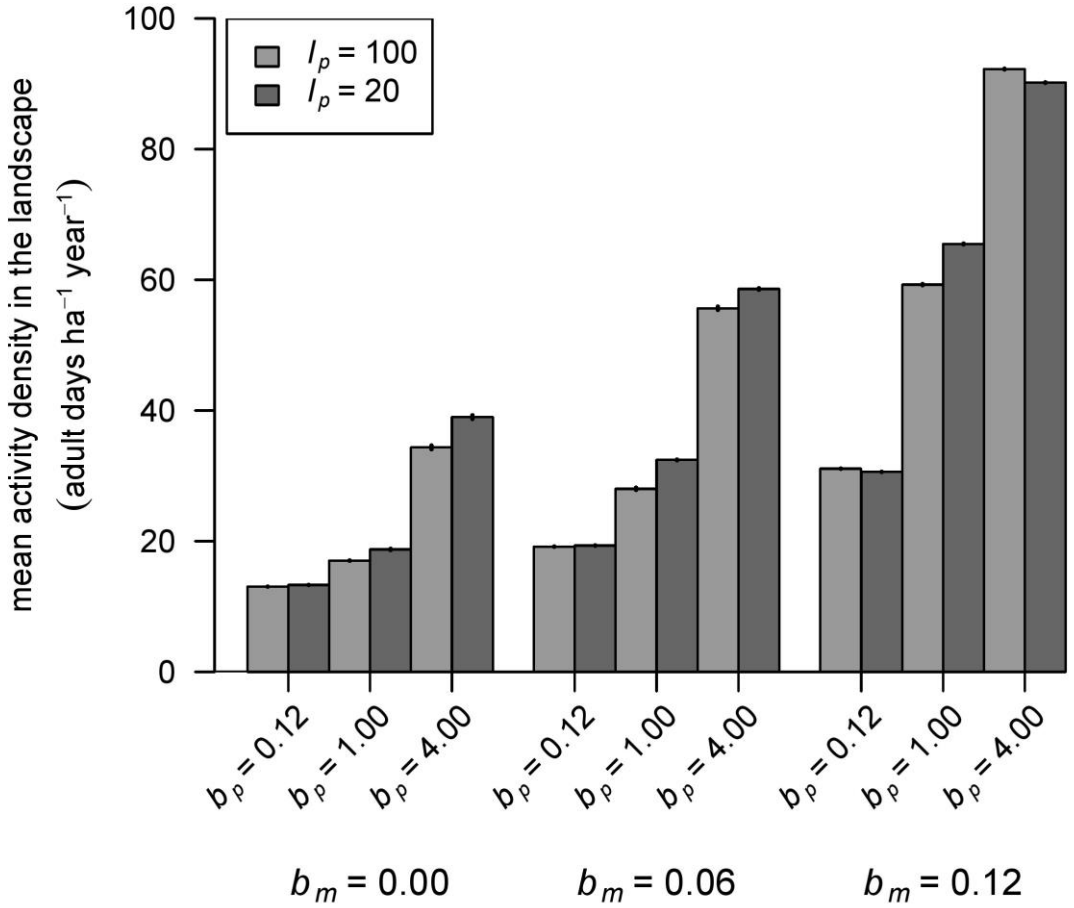


Figure 10. Mean activity density of adults across the entire landscape during years 26-30 of simulations, for 18 hypothetical species with coverage of habitat patches c = 8%. Means (±S.E.) were taken across 30 random seed replicates for each species (note very small error bars). Density generally increases with the egg-laying rate in patches b_p and the matrix b_m. When the mean step length in patches l_p is lower (dark grey bars), mean density in the landscape is higher unless (1) $b_p = b_m$ or (2) b_p, b_m and c are all at their highest values in this study.

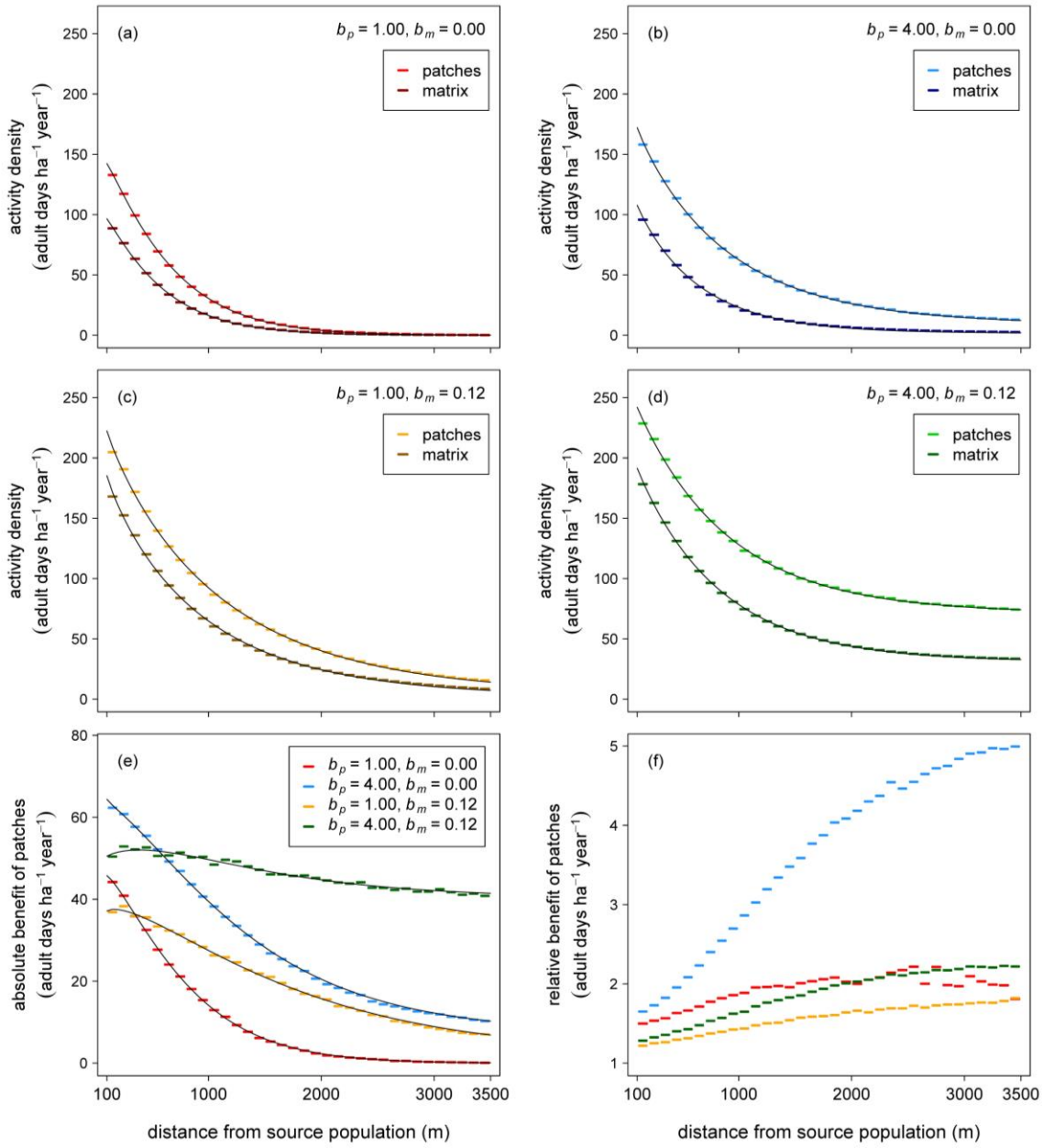
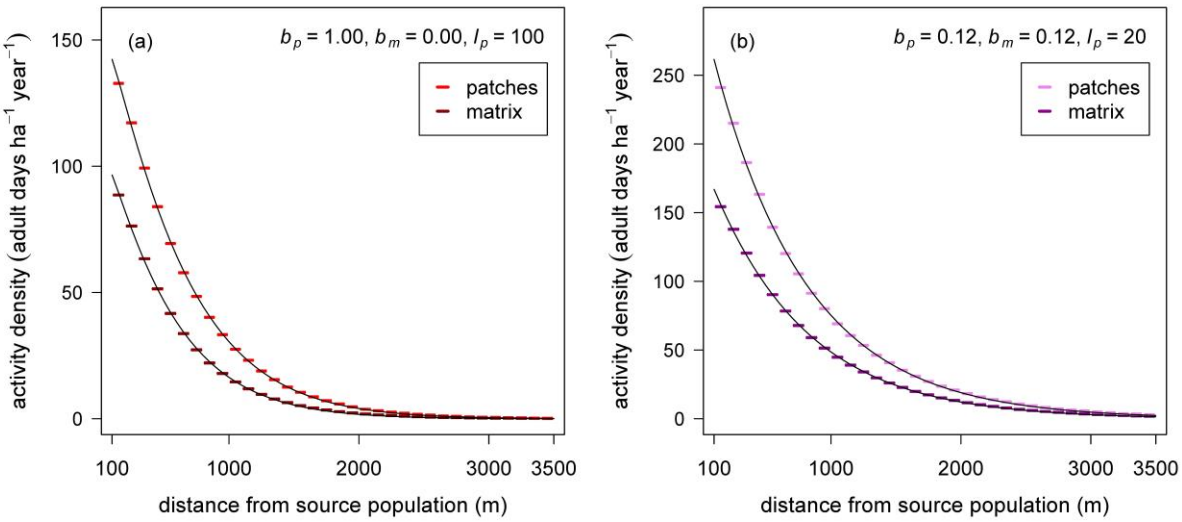


Figure 11. (a-d) Activity density in patches and the matrix as a function of distance from the source population is shown for four hypothetical species. These species were chosen to demonstrate interacting effects of different egg-laying rates in patches b_p and the matrix b_m (see Table 4 for explanations of variable parameters). (e) The absolute benefit of habitat patches as a function of distance for the same four species. These values are obtained by subtracting the darker lines from the lighter lines in panels a-d. Also shown is the absolute difference between the fitted functions (black lines). (f) The relative benefit of habitat patches as a function of distance for the same four species, which is obtained by dividing the lighter lines by the darker lines in panels (a-d). Coverage of habitat patches c is 4% for all species displayed.



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2117 **Figure 12.** Activity density in patches and the matrix as a function of distance from the
2118 source population for (a) a species which lays many eggs in patches (b_p = 1.00) but none
2119 in the matrix (b_m = 0.00) with the same dispersal behaviour in both habitat types (l_p = l_m
2120 = 100), and (b) a species which lays eggs at the same rate in patches and the matrix (b_p =
2121 b_m = 0.12) but takes shorter steps in patches (l_p = 20). Coverage of habitat patches c is
2122 4% for both species displayed.
2123

4.4.2. Increases in absolute benefit of patches due to spatial targeting

Although all species exhibited similarly-shaped functions with respect to distance from the source population (Fig. 11), some would clearly stand to benefit more from spatial targeting than others. For each species I calculated the impact of spatial targeting as the increase in absolute benefit of patches that might be achieved, comparing the benefit of patches at the closest recorded distance to the source population and the benefit of patches infinitely far away (see methods). While downturns in absolute benefit close to the source population were observed for some species (e.g. Fig 11e, yellow and green lines), these tended to be negligible so I used the closest recorded distance to represent the maximum absolute benefit for all species.

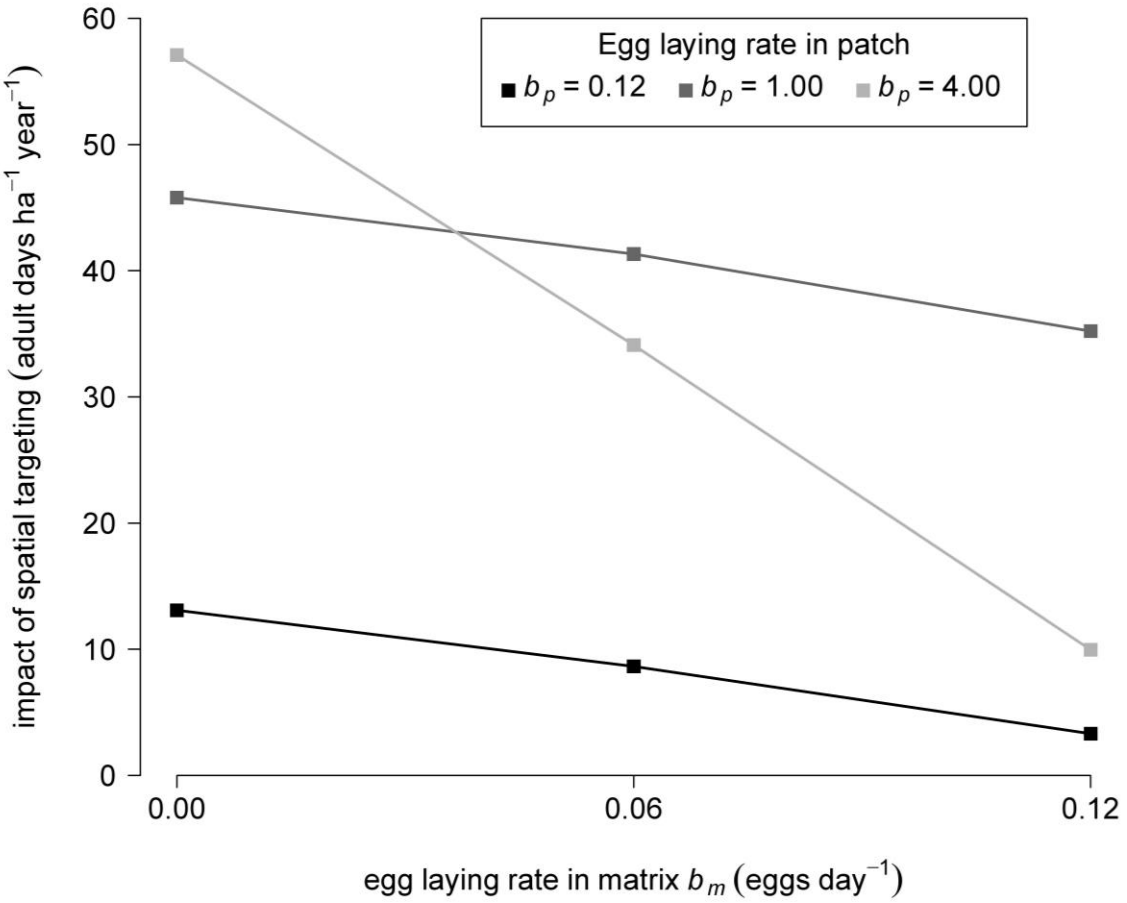
All four of the variable parameters in this model affected the extent to which a species was likely to benefit from spatial targeting. Firstly, increasing the egg-laying rate in the matrix b_m (effectively making a species more generalist) reduced the impact of spatial targeting (compare the maxima and minima of red and yellow lines, Fig. 11e). This effect seems to be brought about by differences in the population dynamics at the furthest distances from the source population: Species which did not reproduce successfully in the matrix ($b_m = 0$) had a high contrast between the benefit of patches close to the source population and patches far away, because distant patches were not colonised (i.e. Fig. 11e, red lines). Conversely, species that laid more eggs in the matrix sustained populations at great distances from the source population, and distant patches provided considerable benefits (Fig. 11e, the yellow line has a positive asymptote while the red line has a zero asymptote). Furthermore, these generalist species experienced reduced benefits in patches close to the source population because density in the matrix was also high (Fig. 11e, yellow lines fall below red lines where distance < 300).

Increasing the coverage of patches c (i.e. representing a species that is more widespread) also reduced the impact of spatial targeting (Figure A7). When coverage was higher, patches far from the source population had greater benefits while patches close to the source population had reduced benefits. Thus my results suggest that the

more generalised and widespread the species, the smaller the difference it makes to locate patches close to the source population.

Increasing the egg-laying rate in patches b_p (i.e. increasing the quality of resources that patches provide for a species) had more complicated results for the impact of spatial targeting. This parameter interacted with b_m and c: increasing b_p increased the impact of spatial targeting unless b_m and/or c also had a high value. For example, when $b_m = 0$, increasing a species' egg-laying rate in patches from a moderate value ($b_p = 1.00$) to a high value ($b_p = 4.00$) led to a slightly increased impact of spatial targeting (Fig. 13; Fig. 11e, compare the red and blue lines). However, when $b_m = 0.12$, increasing b_p from 1.00 to 4.00 lead to a decreased impact of spatial targeting (Fig. 13; Fig. 11e, compare the yellow and green lines). Thus it seems that spatial targeting is more effective for species that experience a higher contrast in reproductive value between patches and the matrix, unless that species is highly abundant throughout the landscape. This could be because eggs/larvae of those abundant species experience higher levels of density-dependent death. As a result the absolute benefits of patches compared to the matrix become limited, and this is especially true for patches close to the source population, where large numbers of eggs are laid by immigrants.

Finally, decreasing the step length in patches l_p (i.e. increasing a species' attraction to patches) consistently increased the impact of spatial targeting (Figure A7). This was the case even if patches had no effect on the rate of reproduction of a species. This effect results from immigrants spending more time, and thus laying more eggs, in patches – especially patches close to the source population.



2174

2175 **Figure 13.** The impact of spatial targeting is shown for nine hypothetical species. The
2176 impact of spatial targeting (Y-axis) represents the difference in absolute benefit between
2177 habitat patches that are as close as possible to the source population and patches that are
2178 infinitely far away. The species shown differ in their egg-laying rate in the matrix (b_m,
2179 X-axis) and their egg-laying rate in patches (b_p, black squares b_p = 4.00, dark grey
2180 squares b_p = 1.00, light grey squares b_p = 0.12). 4% of the landscape comprised habitat
2181 patches for these species (c = 4), and mean step length was the same in patches and in
2182 the matrix ($l_p = l_m$ = 100).
2183

4.5.Discussion

4.5.1. Effects of spatial targeting for different types of species

For the vast majority of hypothetical insect species in this study, patches provided the greatest absolute increase in local density of adults if located near a source population. In a real agricultural landscape AES interventions that increase the reproductive value of an area of land would be like patches described here, while semi-natural habitat would be the source population for many insect species (Öckinger & Smith 2007; Kohler *et al.* 2008). As such, for species that follow the processes of movement, reproduction and density-dependent death included in my model, AES interventions will have greatest benefits if allocated close to existing high-quality semi-natural habitat. It has already been established that the biodiversity of a new patch is maximised by placing it close to other large patches (Diamond 1975). My model adds to this by highlighting that the increase in local biodiversity due to the creation of a patch can also be maximised using the same spatial targeting strategy.

Spatial targeting made a bigger difference to absolute patch benefits for some species than for others, so my results indicate the characteristics of species for which spatial targeting of AES interventions is likely to have the biggest impact. Spatial targeting makes a bigger difference for species that are not generalists in the agricultural landscape, i.e. species that are able to reproduce prolifically in AES interventions but cannot reproduce at all in the matrix. Furthermore, the impact of spatial targeting (as defined in Figure 8) is greater for species that can only reproduce in a smaller proportion of the agricultural landscape. Finally, the impact of spatial targeting is greater for species that adjust their dispersal behaviour and move more slowly in AES interventions. On the other hand, if a species is highly generalist, widespread and disperses randomly, absolute increases in density on AES interventions are almost independent of the source population. Land managers might consider spatial targeting to be less of a priority when aiming to conserve such a species.

4.5.2. Interpretation of field studies of agri-environment scheme interventions

To my knowledge, this is the first population modelling study to provide direct comparisons of biodiversity in patches as compared with the matrix, in cases where both may be affected by "spill-over". As such, my results are useful to interpret results of empirical studies that compare AES interventions with control sites in various landscape contexts (Heard *et al.* 2007; Batáry *et al.* 2011; Scheper *et al.* 2015; Alison *et al.* 2016). For example, Alison *et al.* (2016) found that spatial targeting of grass margins increased their benefits for moths specialised to calcareous grassland habitat, but the same was not true for grassland generalists. My model offers a clear explanation for this result: spatial targeting probably had no significant effect for grassland generalists because they could reproduce successfully across large areas of the agricultural landscape.

However, many empirical studies have revealed effects of land-use context which were not clearly reproduced by my model. For example, Scheper *et al.* (2013) found that AES interventions had increased benefits for insect pollinators in landscapes comprising less than 20% semi-natural habitat. One possible explanation for this mismatch is that my simulations underestimated the level of density-dependent death within populations of real insect species. For hypothetical species with high egg-laying rates across both patches and the matrix, the density of individuals in patches close to the source population was becoming more saturated than for other species (compare the lighter green line in Fig. 11d with the lighter red line in Fig. 11a). This slight saturation in density in patches may have resulted from increased density-dependent death in patches close to the source population. If density in those patches became strongly limited by density dependent death, patch benefits could also be suppressed; indeed the most abundant species I simulated did exhibit downturns in the absolute benefit of patches closest to the source population (Fig. 11e, yellow and green lines). If density dependent death was increased, optimal benefits might occur at an intermediate distances. This would better align with the expectations of Tscharntke *et al.* (2005) as well as the results of several empirical studies (Batáry *et al.* 2011; Scheper *et al.* 2013). However, the literature suggests that density dependence in insect populations is often

2240 weak (Stiling 1988; but see Turchin 1990), so the parameter ranges needed to achieve
2241 such an effect might be unrealistic.

2242 Another explanation for discrepancies between empirical results and my
2243 simulation results is that real insect species, especially pollinators, move and forage in
2244 more complex ways than the hypothetical species I investigated. For example, Heard *et*
2245 *al.* (2007) and Carvell *et al.* (2011) found that sown flower strips led to greater increases
2246 in bumble-bee density when close to large areas of intensive arable land, and not semi-
2247 natural habitat. The authors reasoned that when further from semi-natural habitats,
2248 bumble-bees reacted to a lack of forage by exploiting AES interventions more
2249 thoroughly. Clearly individuals of real insect species make sophisticated decisions when
2250 moving through agricultural landscapes: some Butterfly species use hedgerows and
2251 wood edges to guide their flight (Dover & Settele 2009), while *Maniola jurtina*
2252 perceives and moves toward habitat up to 150m away and prefers known patches
2253 (Conradt *et al.* 2000). Future models could include these sophisticated behaviours to
2254 improve understanding of the mechanisms by which spatial targeting of AES
2255 interventions might affect local density of insect pollinators.

2256 My model included two simple possibilities for insect dispersal behaviour, but
2257 this was sufficient to highlight a key limitation of field studies which measure benefits
2258 of AES interventions based on observations of the adult life-stage. I assumed random-
2259 walk dispersal of adults, but for half of my hypothetical species I added the well-
2260 founded complication that adults move more slowly in patches than in the matrix (i.e.
2261 they are 'attracted' to patches; Schultz 1998; Schultz & Crone 2001; Ovaskainen *et al.*
2262 2008). I found that spatial targeting made a bigger difference for species that moved
2263 slowly in patches, and this was true even if patches did not have increased reproductive
2264 value and were essentially an "ecological trap" (Battin 2004). Clearly spatial targeting
2265 can appear to increase the benefits of AES interventions (Alison *et al.* 2016) even if
2266 AES interventions only affect a species' dispersal behaviour and not reproduction. This
2267 is important because ecological traps in my simulations accentuated density-dependent

death of eggs/larvae, and moving such traps closer to the source population would increase local density of adults, but ultimately decrease overall population size.

My study also demonstrates the need for transparency and consistency in terms of how empirical studies measure the benefits of AES interventions. In my simulations I focussed on absolute benefits but also quantified the relative benefits of patches, and the two measures formed completely different relationships with distance from the source population: The greatest absolute benefit might occur in patches close to the source population, while the greatest relative benefit occurs in patches far away. Empirical studies compare sites with and without AES interventions in a wide variety of ways; Heard *et al.* (2007) make comparisons for bumble-bees based on log-mean density; Scheper *et al.* (2013) make comparisons for insect pollinators across a range of field studies using standardised mean differences; Scheper *et al.* (2015) make comparisons for bumblebees and solitary bees based on log response-ratios (relative increases over time), while Alison *et al.* (2016) make comparisons for moths based on raw counts (in log-link mixed effects models). Clearly when designing a study to optimise the placement of AES interventions, the way in which benefits are measured should be given careful consideration. Even log-transforming density values could drastically change the results of field studies, as this is equivalent to switching from absolute benefit of AES interventions to relative benefit.

4.6.Conclusions

I show that spatial targeting of AES interventions will have different effects on the density of adult insects depending on the characteristics of the species in question. However, for insect species that (1) reproduce more prolifically in AES interventions than the matrix, (2) have simple random dispersal behaviours and (3) have populations that are not strongly limited by density dependent death, land managers are likely to maximise absolute increases in density by allocating AES interventions close to source populations (usually semi-natural habitat; Öckinger & Smith 2007; Kohler *et al.* 2008). Furthermore, spatial targeting is likely to be most critical for species which can only reproduce in the source population and some low coverage of AES interventions. Spatial

targeting will make little difference to relatively generalist species, even if they also have large populations in semi-natural habitat.

I have interpreted the simulation parameters in this study as the characteristics of species, but they are just as easily interpreted as characteristics of different landscapes. For example, a landscape with a high reproductive value of patches might represent a high investment in the quality of resources in AES interventions. Similarly, a high reproductive value in the matrix could represent a background land-use of low agricultural intensity such as organic farming. From the landscape perspective, I show that spatial targeting should take a higher priority in high-contrast landscapes; that is landscapes where AES interventions form a very low coverage (~2%) and are of high reproductive value, while the rest of the agricultural landscape is intensively farmed and inhospitable.

However, my study also presents two warnings for land managers and researchers interpreting the benefits of spatial targeting for insect species. Firstly, AES interventions may appear to be more beneficial with spatial targeting even if they only affect the dispersal of individuals. Conservationists often aim to increase overall density as well as local density, so advice from studies that exclusively monitor adult life-stages should be received critically. By monitoring both adult and juvenile stages of the life-cycle, future empirical work might better understand whether AES interventions facilitate reproduction of insect species (Westphal, Steffan-Dewenter & Tscharntke 2009). Secondly, I show that the way in which a study measures the benefits of AES interventions can profoundly affect conclusions about spatial targeting of AES interventions. I argue that future studies should focus on absolute increases in density. This is because improvement of ecosystem services is an increasingly recognised conservation goal, and it seems likely that processes such as pollination and nutrient cycling will scale with absolute numbers of individuals rather than relative numbers.

Chapter 5: Discussion

Chapters 2&3 of this thesis present two of the most robust case-studies to investigate the interaction between semi-natural habitat and the impact of AES interventions (Alison *et al.* 2016, 2017). Using evidence from both of my field studies in the context of existing literature, I can make suggestions about the effect of spatial targeting of AES interventions for different species groups and intervention types (see 5.1. Evidence from field studies). Chapter 4 presents an individual-based model which is ground-breaking in terms of its applicability to empirical studies on the spatial targeting of AES interventions. Interpretation of this model in the context of field data allows a greater understanding of the mechanisms by which spatial targeting affects the outcome of AES interventions (see 5.2. Mechanisms by which agri-environment schemes interact with source populations). While the enclosed studies are not without their limitations, ultimately I produce clear advice for land managers who may be interested in the conservation of moths and other species groups with which they coexist (New 2004). This advice is summarised in light of two biodiversity objectives – to conserve species based on intrinsic values and to increase the provision of ecosystem services (see 5.3. Summary of advice for land managers).

5.1.Evidence from field studies

My two field studies (Chapters 2&3) represent a substantial contribution to the limited evidence base about effects of the landscape context on the outcome of AES interventions (Alison *et al.* 2016, 2017). To my knowledge these are the first such studies to focus on night flying Lepidoptera (moths), which are potentially important nocturnal pollinators (Macgregor *et al.* 2014, 2017) and are declining in the UK (Conrad *et al.* 2006; Fox *et al.* 2014). Unlike many field studies of AES interventions (Kleijn & Sutherland 2003), they compare adequately replicated treatment sites (16 in Chapter 2, 32 in Chapter 3) to the same number of carefully paired control sites. Critically, my field studies are among the few which test for interactions between the benefits of AES interventions and the surrounding landscape context (see also Rundlöf & Smith 2006;

Heard *et al.* 2007; Concepción, Díaz & Baquero 2008; Carvell *et al.* 2011; Concepción *et al.* 2012; Scheper *et al.* 2015). Thus, in Chapter 2 I provide evidence that for priority insect groups, AES interventions might be most effectively located close to existing semi-natural habitat (Alison *et al.* 2016). Furthermore, unlike most field studies of AES interventions, mine compare biodiversity with that on that on high-quality semi-natural habitat. Thus, in Chapter 3 I provide fresh evidence that biodiversity on AES interventions may compare favourably with that on semi-natural grassland (Alison *et al.* 2017) and not just that on intensive farmland (Fuentes-Montemayor, Goulson & Park 2011; Pywell *et al.* 2012).

Unfortunately it was not possible for me to survey grass margins, restored grassland and appropriate control sites all in the same year. However, a crude comparison of results of Chapters 2&3 suggests that grassland restoration has greater potential to increase the abundance and species richness of moths than the creation of grass margins. I have combined moth counts from the two study years for a preliminary comparison of the two AES intervention types (Appendix A7, Figure A8, Table A12): I found that grassland restoration generally had greater benefits for moths than creation of grass margins, although this difference was only significant for CG moths. However, there were considerable limitations when making comparisons based on light trap data across two separate field studies (see Appendix A7 for details). Future work might compare these two interventions using more robust methods, but my priority here was to look at the interaction between AESs and the landscape context.

With a focus on calcareous grassland moths, Chapter 2 reveals a positive relationship between the benefits of AES grass margins and the extent of calcareous grassland habitat nearby. These results appear to contradict those from previous work, which has often shown that AES interventions may be more effectively located at distance from semi-natural habitat. For example, Heard *et al* (2007) found a positive relationship between the coverage of arable land and benefits of sown forage patches for bumblebees. Furthermore, recent high-power meta-analyses found that benefits of AES interventions are generally greater in landscapes with <20% semi-natural habitat than in

landscapes with >20% semi-natural habitat (Batáry *et al.* 2011; Scheper *et al.* 2013). I suspect that the discrepancy in results between previous studies and Chapter 2 may have occurred because previous studies focussed on broad subsets of wildlife, while I focussed on species specifically associated with semi-natural habitat. Taken in the context of previous work, my results suggest that spatial targeting close to source populations is more of a priority for specialised species which may be of increased conservation concern. This concept was proposed earlier by Kleijn *et al.* (2011), but I have provided some of the clearest evidence to date in support of it.

Unlike Chapter 2, Chapter 3 did not provide evidence that AES interventions might be most effectively located close to existing semi-natural habitat. Instead, the frequency of indicator wildflowers emerged as an important determinant of the abundance of calcareous grassland moths on AES-restored grassland fields (Alison *et al.* 2017). Taken together, the results of the two field studies generate the hypothesis that different types of AES intervention interact with the landscape context in distinct ways. While this hypothesis is also broadly supported by the results of the individual-based model put forward in Chapter 4, future studies might attempt to test it directly.

My field studies supplement the high-power meta-analyses that have, so far, shaped the debate about where AES interventions can make the biggest difference to biodiversity (Batáry *et al.* 2011; Scheper *et al.* 2013; see Chapter 1 for overview). Meta-analytical approaches are subject to publication bias; around three quarters of observations in the study of Batáry *et al.* (2011) corresponded to organic farming, suggesting that many types of AES intervention were probably underrepresented. It is also likely that certain types of AES intervention are correlated with specific landscape features, which could confound effects of the landscape context in meta-analyses. On the contrary, my field studies avoided such problems. This is because my data collection protocols were designed to look at the effects of specific types of AES interventions across a range of distances to semi-natural habitat. Furthermore, where previous studies have considered the landscape context using coverage of semi-natural habitat or arable land within a 1km buffer (Heard *et al.* 2007; Batáry *et al.* 2011; Scheper *et al.* 2013) my

field studies used connectivity measures. In this way I summarised information on distances to and areas of all known semi-natural habitat patches. Previous studies have shown that connectivity measures outperform simple buffer measures in predicting colonisation events of butterflies, especially in highly fragmented landscapes (Moilanen & Nieminen 2002). Given that observations of AESs tend to be made in landscapes with <20% semi-natural habitat (Batáry *et al.* 2011), use of connectivity measures could improve the capacity for future studies to relate AES benefits to landscape features.

It would have been possible to investigate the effects of AES interventions on population demographics of a few specific moth species in this PhD project. However, I opted to collect data on adults of all moth species that came to light traps. My study design was in many ways fit for purpose: For example, huge amounts of moth individuals (almost 20,000) could be recorded during a short project, producing results relevant to UK moth biodiversity as a whole. Furthermore, changes in ecosystem services, such as pollination, would be likely to scale with the local abundance of adult moths regardless of underlying mechanisms (Kleijn *et al.* 2011). However, by defining "benefits" of AES interventions as increases in the local abundance and species richness of insects at the adult stage, I may have foregone useful insights relevant to reversal of large-scale biodiversity declines. For example, Kleijn *et al.* (2011) identified that conservation evaluation studies focus on local effects which are not relevant to conservation objectives formulated at the national or continental level. The authors recommended that future studies evaluate how conservation interventions change species' population demographics, such that results might be scaled up for relevance to conservation policies (Kleijn *et al.* 2011). My individual-based model revealed some simple demographic and movement processes which might give rise to observations such as those I made in the field. However, future studies should strive to survey species at all stages of their life cycle to better understand the effects of AES interventions on the population as a whole.

5.2. Mechanisms by which agri-environment schemes interact with source populations

My individual-based model (Chapter 4) represents the first of its kind to test how the benefits of AES interventions depend on distance from a source population. Crucially, I compared the activity density of individuals in AES interventions and the surrounding matrix of my simulated landscapes. This imitated the approach of empirical studies, including Chapters 2&3 of this thesis, which have measured the benefits of AES interventions using similar methods. By simulating larval and adult life-stages of various hypothetical species of Lepidoptera, I was able to shed light on the mechanisms by which spatial targeting may affect the benefits of AES interventions.

A critical finding was that AES interventions were most beneficial when located close to the source population for the vast majority of hypothetical insect species. As such, my simulations highlighted two possible scenarios which produce similar results to those observed for calcareous grassland moths in Chapter 2. In one of these scenarios AES interventions provided some increase in reproductive value, but in the other AES interventions just caused individuals to move slowly and conferred no increase in reproductive value (i.e. interventions were "ecological traps"). This result shows that spatial targeting of AES interventions toward semi-natural habitat might increase the local abundance of adult moths without providing any benefit to the population as a whole. Studies that observe changes in the local abundance of insects at the adult-stage (e.g. Alison *et al.* 2016) might heed this result when producing advice for land managers.

However, I also found that when AES interventions had both high coverage and very high reproductive value for a simulated insect species, their benefits did not decline steeply with distance from the source population. This key result offers an explanation as to why Chapter 3 found no significant interaction between the benefits of restoring arable fields to species-rich grassland and connectivity to calcareous grassland habitat. Unlike grass margins, restored grassland fields supported high abundances of calcareous grassland moths and probably had considerable reproductive value for that group

(Alison *et al.* 2017). Thus, contingent on the assumptions of my individual based model, the benefits of restored grassland fields would be less strongly affected by distance to source populations than grass margins (Fig. 11e, green line represents benefits of restoration of restored grassland while the yellow line represents benefits of grass margins).

Previous studies have observed greater benefits of AES interventions that are more isolated from semi-natural habitat (Batáry *et al.* 2011; Scheper *et al.* 2013). This is surprising because semi-natural habitat harbours source populations of insect species and might be critical for the colonisation of AES-created habitats (Öckinger & Smith 2007; Kohler *et al.* 2008). Nonetheless, spill-over of individuals from semi-natural habitat is often used an explanation for these counter-intuitive results. For example, Tscharntke *et al.* (2005) argued that biodiversity is high everywhere in landscapes with high cover of semi-natural habitat, such that the effects of AES interventions are obscured. However, my individual-based model, which included spill-over from a source population, did not reveal increased biodiversity benefits of isolated AES interventions. Thus I show that the observations of previous meta-analyses (Batáry *et al.* 2011; Scheper *et al.* 2013) might not be underpinned by simple source-sink population dynamics, but instead by complicated movement and foraging behaviours. For example, Heard *et al.* (2007) reasoned that when further from semi-natural habitats, bumble-bees reacted to a lack of forage by exploiting AES-provided resources more thoroughly. I argue that future studies finding that the benefits of AES interventions are higher in landscapes with little semi-natural habitat should look beyond simple source-sink dynamics when seeking to explain their results.

5.3.Summary of advice for land managers

I propose that the ultimate objectives of AESs are (1) the enhancement of threatened aspects of biodiversity that have intrinsic value or are of conservation concern and (2) the enhancement of functional aspects of biodiversity to aid sustainable delivery of a wide range of ecosystem services. These two objectives have been put forward in previous studies (Kleijn *et al.* 2011; Ekroos *et al.* 2014) and are reflected in some

official AES documentation (Natural England 2012). Recent evidence has highlighted that the bulk of ecosystem services may be provided by a subset of common species, as opposed to species which are rare or threatened (Kleijn *et al.* 2015; Winfree *et al.* 2015). As such, it is likely that the optimal management decision to conserve threatened species will often differ from the optimal decision to increase ecosystem services. Following this, I summarise the evidence produced by this thesis from two perspectives: one which prioritizes the conservation of threatened species based on intrinsic values, and another which prioritizes the sustainable provision of ecosystem services. Policy advice based on my field studies has previously been summarised for non-specialists in my submission to the UK Parliament's Environmental Audit Committee in 2016 (Appendix P2).

I produce advice for land managers primarily interested in the conservation of threatened species using evidence about moths that are specialised to calcareous grassland (CG). This is because CG is recognised as a priority habitat across much of Europe (CEU 1992) and may be of particular importance for declining macro-moth species, the larvae of which to feed on plants adapted to open, nutrient poor habitats (Fox *et al.* 2014). On the other hand, I produce advice relevant to ecosystem services using information about all moth individuals, most of which can be identified as highly abundant habitat generalists. Ideally I would focus on a subset of species that are known to provide ecosystem services following Dicks *et al.* (2015). However, the evidence about which moth species provide ecosystem services, for example pollination, is currently limited (Macgregor *et al.* 2014). The enclosed studies were designed specifically to produce advice for land managers, but policy advice based on one or a few scientific studies should be interpreted with care. Systematic reviews and synopses are both critical steps to produce unbiased, evidence-informed environmental policies (Dicks *et al.* 2014; Dicks, Walsh & Sutherland 2014).

Some land managers strive to conserve rare or threatened species, but are only able to create small patches of grassland on arable fields. Furthermore, land managers may not have the resources to enhance the plant community on that grassland to provide host plants for rare insect species. Under these circumstances, I recommend that AES

interventions be placed as close as possible to source populations of the target species. Spatially targeting AES interventions in this way should make AES foraging resources more accessible, to maximise increases in local abundance of priority insect groups (Alison *et al.* 2016). Nonetheless, non-tailored AES interventions may not provide substantive breeding resources for species of conservation concern, and could even represent "ecological traps". As such, land managers should take care to confirm that AES interventions provide useful resources for the target species group, e.g. host-plants for priority moth species, before adopting this spatial targeting recommendation.

Land managers most interested in rare or threatened species should, where possible, use evidence-based management to restore plant communities that are typical of semi-natural habitat. I endorse the recommendation of previous studies that plant community enhancement measures, such as spreading green hay or sowing flower mixtures, could help to maximise benefits of AES interventions for priority insect species (Woodcock *et al.* 2010; Pywell *et al.* 2012). When such management is adopted across entire fields, the abundance and species richness of priority insect groups can be as high as that found on existing semi-natural habitat (Alison *et al.* 2017). Furthermore, the frequency of indicator wildflowers can be used as a crude indicator of the quality of AES interventions for priority insect species. When it comes to AES interventions that restore high-quality habitats at large scales, for example restoring arable fields to species-rich grassland, spatial targeting may be less important than for generic interventions such as grass margins. My explanation for this, based on my individual based model, is that low-quality AES interventions often represent sink habitats – that is habitats which have some reproductive value but are highly dependent on colonists from source populations. On the other hand, high-quality AES interventions are source habitats, which are able to support viable populations even at great distances from source populations.

Land managers interested in provision of ecosystem services such as pollination might be most interested in increasing the abundance of common species (Kleijn *et al.* 2015; Winfree *et al.* 2015), which are the main beneficiaries of some types of AES

intervention. For example benefits of grass margins for grassland generalist moths are substantial and do not depend strongly on connectivity to semi-natural CG habitat (Alison *et al.* 2016). Clearly AES interventions have great potential to increase the abundance of ecosystem service providers, and this might lead to increases in yield of pollinator-dependent crops nearby (Albrecht *et al.* 2007; Pywell *et al.* 2015). I advise that small-scale, generic AES interventions such as grass margins should not be overlooked when it comes to the provision of ecosystem services. I found no indication that spatial targeting of AES interventions relative to CG habitat would increase benefits for moths in general. In fact, following the meta-analyses of Batáry *et al.* (2011) and Scheper *et al.* (2013) the optimal placement of AES interventions to provide ecosystems services may be in landscapes with 1-20% cover of semi-natural habitat. However, I emphasise that while targeting AES interventions in such a way may lead to greater increases in the local abundance of ecosystem service providers, this does not necessarily correspond to improved population demographics (e.g. increased birth rates). Even so, ecosystem services are likely to be most in demand in agriculturally profitable areas which are likely to have a high coverage of intensive farmland (Kleijn *et al.* 2011).

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Appendices

Appendix A1: Spatial analysis for site selection

Geographic datasets used during spatial analysis were (1) polygons of Environmental Stewardship fields, including details of all AES management happening within each field (Natural England Data Mobilisation and Analysis Team, Reading, UK, retrieved: 10th May 2014), (2) a 25×25 m raster of arable land across Hampshire (extracted from 2007 UK Land Cover Map, Morton *et al.* 2011), (3) polygons of calcareous grassland (CG) in Hampshire (from Hampshire County Council http://www3.hants.gov.uk/biodiversity/hbic, retrieved: 20th February 2014), (4) polygons of CG in surrounding counties and (5) polygons of Site of Special Scientific Interest (SSSI) boundaries in Hampshire (both from http://www.naturalengland.org.uk/publications/data, retrieved: 20th February 2014).

Appendix A2: Calculation of connectivity to calcareous grassland

Polygons of coverage of CG in the study area were used to produce a 100×100 m raster, with the value of each cell corresponding to the % cover of CG within it. Connectivity to CG was calculated to the same resolution, with the connectivity of each cell being a function of the distances to and % coverage of all other cells in the landscape. Assuming a negative exponential dispersal kernel (Hanski 1994), connectivity *C* of each cell *i* was calculated such that

$$C_i = \sum_{j \neq i} A_j e^{-\alpha d_{ij}} \quad (1)$$

where *A* is the % coverage of CG habitat in cell *j* and d_{ij} is the Euclidian distance (km) between the centres of cells *i* and *j*. The parameter α scales the effect of d_{ij} on dispersal, and following Hodgson *et al.* (2012) the mean distance is 2/α. For the purposes of this study, the multiplier of α = 2 was selected to represent a mean distance of 1km. I extracted the connectivity to CG of each trap location from the raster using the *R* package *maptools* (Bivand & Lewin-Koh 2014).

Mark-release-recapture (MRR) studies on common farmland moth species have found mean distances covered between first capture and first recapture to be up to 0.65 km (Merckx *et al.* 2009a, 2010a). However, the maximum distance between any two of the capture sites in both of these studies was only 1.44 km, therefore lifetime dispersal of the species studied is likely to be greater (Schneider 2003). A larger-scale MRR of Slade *et al.* (2013) on forest fragments around Wytham Woods, UK, had a maximum pairwise trap distance of 4.13km. In this study there were some highly mobile species which had modelled mean distances moved within one week that were greater than 1km, but these were woodland specialists that were rarely caught in my study. Macro-moth species in Slade *et al.* (2013) were more generally expected to have a net displacement of between 250 and 500m per week; given the scale of their study, I believe that 1km is a reasonable approximation of what the mean lifetime displacement might be for macro-moth individuals in my study, hence I use a mean distance of 1km in my dispersal kernel.

Appendix A3: Moth surveys and species specialism methodology

Macro-moth surveys were carried out by J Alison. Trapping was carried out on good weather nights with min temperature >10˚C, max wind speed <20km/h and max precipitation risk <50% (following Merckx *et al.* 2009a) according to http://metoffice.gov.uk. Surveys were carried out using up to ten Heath style actinic light traps (15w) fitted with solar sensors for automatic activation/deactivation at sunset/sunrise. Traps were recovered in a different order each morning, with the first trap being counted at sunrise. Before being released at the site of capture, moth individuals were identified on-site or photographed for later identification using Waring and Townsend (2009) and Sterling & Parsons (2012; micro-moths only recorded in 2015 study, Chapter 3). Where vegetation was tall enough to partially conceal the actinic bulb, traps were elevated to full visibility using purpose-built collapsible wooden stands. Locations of traps were recorded using a GPS device. Survey sites were widely-distributed across the landscape, and the time windows in which they were accessible for survey varied considerably due to weather and agricultural management.

Species specialism of each moth species was determined based on the "habitat" section of its description in Waring and Townsend (macro-moths; 2009) or Sterling & Parsons (micro-moths; 2012). A species was considered to be a "CG species" if occurrence on "calcareous/chalk/limestone" and "grassland/grass/downland/meadows/pasture" were listed, but on the condition that the species was not "ubiquitous" and was not explicitly stated to occur in "woodland" or on "many/most/wide variety" of habitats. Remaining species could be considered "grassland species" based on the same criteria except without mention of occurrence on "calcareous/chalk/limestone" geology. "Other species" were all species which did not fall into the two previous categories.

During the 2015 field study (Alison *et al.* 2017; Chapter 3), I identified six species of micro-moth that were not were not specified to occur on "many/most/wide variety" of habitats in Sterling & Parsons (2012) despite strong evidence to the contrary. These species, *Chrysoteuchia culmella, Crambus perlella, Agriphila straminella,*

Agriphila tristella, *Agriphila inquinatella* and *Agriphila geniculea* (Agassiz, Beavan & Heckford 2013), all belonged to the sub-family Crambinae. They accounted for 2,614 of the individuals recorded in my study, were present in substantial numbers on arable fields and are distributed nationwide. As such, I sought a second opinion from an author of Sterling & Parsons (2012) on these species, which confirmed that they are "generally widespread and occur in most grassland habitats, or habitats with grassy situations" (Mark Parsons, pers. comm. 11th August 2016). I took this extra information into account so that these species were not incorrectly classified as CG moths.

Appendix A4: Area estimations for land management types

Using ArcGIS 10.1 (ESRI, Redlands, California), land in Hampshire was divided into four categories based on connectivity to CG (henceforth referred to as "connectivity bands"; after $\log_2$ transformation and centring on the mean connectivity of survey locations the four connectivity bands were: $C < -2$, $-2 \leq C < 0$, $0 \leq C < 2$, and $C \geq 2$). Using the geographical datasets outlined in Appendix A1 (or Chapter 3.3.1. for my 2015 field study), I extracted the total area of arable land, AES interventions (as defined during site selection) and CG habitat in each of the four connectivity bands.

In order to estimate the proportion of arable land in Hampshire that could be considered "margin" in the context of my study, I took the mean size of all the arable fields containing AES interventions in Hampshire: 0.136km^2. I assumed fields were square in shape, and calculated the length of one side to be $\sqrt{0.136} = 0.369\text{km}$. I assumed that land up to 10m from the field boundary was "margin" because (1) my "margin" traps had been placed 5m from the field boundary and (2) the AES interventions I studied ranged from being 6m wide to ~20m wide. Assuming that any land further than 10m from the field boundary was "centre", I took $(0.369\text{km} - 0.02\text{km})^2 = 0.122\text{km}^2$ to give the area of "centre" on the average field. Subtracting the area of "centre" from the total area of an average field gave the area of "margin": $0.136 - 0.122 = 0.014\text{km}^2$. I divided the area of "margin" on the average field by its total area, to determine that "margin" accounts for 10.5% of the area of the average field. I then proceeded under the assumption that 10.5% of arable land is "margin" across the entire landscape in Hampshire.

To estimate the area of control margins in each connectivity band I took 10.5% of the total arable area in that band ("margin" area) and subtracted the actual area of AES interventions in that connectivity band. At this stage I had estimated the existing area of AES interventions, control margins, arable centre and CG habitat in each connectivity band.

Finally, I estimated the areas of AES interventions and control margins in each connectivity band under a scenario in which AES interventions were maximally targeted towards CG habitat. This was done by taking the total area of AES interventions across all connectivity bands, and then reallocating it to fill arable "margin" in the highest available connectivity band (Table A4). If the "margin" in the highest connectivity band became saturated with AES interventions, I continued allocation in the next highest band and so on. Within each connectivity band, the post-targeting area of control margins was estimated by subtracting the area of AES interventions from the arable "margin" area. Areas of CG habitat and arable field centre in each connectivity band were unchanged in the targeted scenario.

Appendix A5: Plant surveys

The reference list of CG indicators that I recorded during surveys was designed to test whether restored grassland can be considered Biodiversity Action Plan priority habitat (displayed below, NE 2010). Quadrats were placed strategically around the moth trap location: four quadrats were placed 10m from the trap location forming a square around it, and the remaining six quadrats were placed in a large 'w' centred on the trap and extending up to 50m from it at either end. I aimed to avoid carrying out plant surveys when a field had recently been cut or heavily grazed, but in a few cases this wasn't possible due to access restrictions. For authorities see Stace (2010):

Stachys officinalis (Betony)

Lotus corniculatus (Bird's-foot-trefoil)

Geranium sanguineum (Bloody crane's-bill)

Carlina vulgaris (Carline thistle)

Campanula glomerata (Clustered bellflower)

Helianthemum nummularium (Common rock-rose)

Primula veris (Cowslip)

Filipendula vulgaris (Dropworts)

Succisa pratensis (Devil's-bit scabious)

Euphrasia sp. (Eyebright)

Linum catharticum (Fairy flax)

Knautia arvensis (Field scabious)

Gentiana sp. (Gentians)

Centaurea scabiosa (Greater knapweed)

Viola hirta (Hairy violet)

Campanula rotundifolia (Harebell)

Plantago media (Hoary plantain)

Helianthemum canum (Hoary rock-rose)

Hippocrepis comosa (Horseshoe vetch)

Anthyllis vulneraria (Kidney vetch)

Galium verum (Lady's bedstraw)

Origanum vulgare (Marjoram)

Polygata sp. (Milkworts)

Pilosella officinarum (Mouse-ear hawkweed)

Family Orchidaceae (Orchids)

Leucanthemum vulgare (Ox-eye daisy)

Astragalus danicus (Purple milk-vetch)

Ononis repens (Restharrow)

Leontodon hispidus/saxatilis (Rough/lesser hawkbit)

Sanguisorba minor (Salad burnet)

Serratula tinctoria (Saw-wort)

Scabiosa columbaria (Small scabious)

Asperula cynanchica (Squinancywort)

Cirsium acaule (Stemless thistle)

Arenaria serpyllifolia (Thyme-leaved sandwort)

Clinopodium vulgare (Wild basil)

Thymus polytrichus (Wild thyme)

Blackstonia perfoliata (Yellow-wort)

Appendix A6: Imperfect transformation of entities in individual-based model

The individual-based modelling platform I used, *ppsimulator*, requires the user to specify the class of entity which is affected by each stochastic process. As such, in order for adults in patches and adults in the matrix to be associated with different parameters (e.g. b_p vs. b_m), they needed to be identifiable as different classes and affected by different processes. Thus, I included two processes that changed the class of adults based on whether they were inside or outside patches: (1) Adults outside patches (Fig. 9, class 1) that were located within 25m of the centre of a patch became adults inside patches (class 2) at a very high rate. (2) Adults inside patches (class 2) that were actually located outside of a patch, but still within 200m of a patch, became adults outside patches (class 1) at a very high rate. The 200m limit was used because if the spatial scale of the process were to increase, the computation time would become disproportionately longer. I increased the rates of these transformation processes to as high a value as possible while still allowing simulations to finish within 30 days.

Thorough inspection of simulation results showed that a few individuals were identifiable as class 2 when outside of habitat patches. On the other hand, there were barely any instances of class 1 individuals being inside patches. When calculating activity density in patches and the matrix I used the class of individuals to indicate their location, and this indication was imperfect. While I suspect that the outcome of this caveat for my analysis and inference were probably negligible, immediate effects would be as follows:

1) In calculations of activity density, very slightly more individuals would have been counted as inside patches than were actually located inside patches. This was because I used individuals' classes as an (imperfect) indicator of their location. I inspected activity density where patches and the matrix were functionally identical (i.e. $b_p = b_m$ and $l_p = l_m$) and found that this was not a significant problem.
2) Where $b_p > b_m$, slightly more eggs would have been laid in the matrix than would be expected in a model without the caveat. This is because a minute number of

individuals behaved as though they were in patches (i.e. they laid more eggs) when they were actually in the matrix. It is worth noting that those eggs would also be exposed to low levels of density dependent death, which would make them likely to survive to adulthood.

Appendix A7: Comparing increases in moth abundance caused by grass margins and restoring arable fields to species-rich grassland

Introduction

This thesis presents two field studies which assess the outcomes of two different agri-environment scheme (AES) interventions for the abundance of moths. The first study carried out in 2014 focused on grass margins, while the second study in 2015 focused on restoring arable fields to species-rich grassland. Grass margins are ubiquitous, small-scale AES interventions that create small strips of grassland on the edges of arable fields. On the other hand, restoring arable fields to species-rich grassland targets entire arable fields, using specialised management to restore communities of plants and insects usually found on semi-natural habitats such as calcareous grassland (CG). While the two studies were carried out in different years, the moth survey protocols used within them were largely the same (see Appendix A3). Both studies compare sites with AES interventions to carefully paired sites without AES interventions (control sites). Furthermore, the two studies were carried out at a similar time of year (summer) in similar study regions, with some farms being visited in both 2014 and 2015. Because of the parallels between these studies, an opportunity exists to combine the data across both years and compare the effectiveness of grass margins and grassland restoration to restore the abundance of moths.

I merge two datasets of the abundance of moths in three distinct habitat specialism groups (calcareous grassland moths, grassland generalist moths and other moths) on sites with and without AES interventions. I test the hypothesis that restoring arable fields to species-rich grassland leads to greater increases in the abundance of moths than the creation of grass margins. In doing so I hope to produce advice for land managers faced with the decision to invest in either high-maintenance AES interventions such as restoring arable fields to species-rich grassland, or generic interventions such as grass margins.

Methods

I used data from moth surveys carried out in 2014 on the edges of 16 arable fields with grass margins and 16 arable fields without grass margins (control sites). All fields in the 2014 study were surveyed on three separate occasions, so count data were available from a total of 96 traps. These data were combined with data from moth surveys carried out in 2015 at the centres of 32 fields restored to species-rich grassland and 32 arable fields (control sites). All fields in the 2015 study were surveyed on two separate occasions, but two surveys suffered technical faults (one on a restored grassland field and one on an arable field) so count data were available from a total of 126 traps. After merging the 2014 and 2015 datasets, count data were available from a grand total of 222 traps.

While the moth surveys used in 2014 and 2015 studies were methodologically very similar, they were conducted in slightly different regions at slightly different times of the year. To minimise the effects of such differences on my conclusions about the effectiveness of the two AES interventions, I excluded any individuals belonging to species which only occurred in one of the two field studies. The remaining moth individuals in each trap were divided into three distinct habitat specialism groups following Appendix A3, so there were 666 observations (counts) in my combined dataset. These observations were used as the response variable in generalized linear mixed-effects models (GLMMs) in the package *glmmADMB* (Skaug *et al.* 2015). Negative binomial error structures were used to model overdispersion in count data. To account for non-independence in the data caused by repeat samples of fields and temporal autocorrelation, random intercepts were included for survey field and survey date.

Three variables were used as fixed effects: "species specialism", "presence of AES" and "type of AES". Species specialism was a factor with three levels corresponding to counts of grassland generalist species (base level), CG species and other species from each trap. Presence of AES was a factor detailing whether an observation was made on a site with an AES intervention or on a corresponding control

site. This factor had two levels: absent (base level) or present. Type of AES was a factor with two levels detailing whether an observation was made in 2014 corresponding to grass margins (base level), or in 2015 corresponding to grassland restoration. It is worth noting here that differences in baseline abundance between the two levels of this factor could be affected by inter-year variation. Nonetheless, I am interested in differences in the effect of AES interventions, which may be less likely to show inter-year variation than baseline abundance. I assume that if one of the years was poor for moths on AES interventions, it was proportionally poor for moths on control sites.

My hypothesis states that the effects of the presence of an AES intervention on moth abundance might differ between intervention types. Furthermore, the difference between the effects of the two intervention types could depend on the habitat specialism of the group of moths in question. For these reasons I included a three-way interaction term in the model, so that the fixed effects structure of my model was *moth counts ~ species specialism * presence of AES * type of AES.* I used Wald *Z*-tests to determine whether key parameters differed significantly from zero.

Results

A total of 124 species of macro-moth were recorded at least once during field studies in both 2014 and 2015, of which 21 were grassland generalist species and 8 were CG species. The remaining 95 species were either associated with other habitats, such as woodland, or of no strong habitat association. A total of 9,372 macro-moth individuals of these species were recorded on sites with AES interventions and/or appropriate control sites across both field studies. Of these individuals 3,479 (37.1%) belonged to grassland generalist species, 375 (4%) belonged to CG species and 5,518 (58.9%) belonged to other species.

The presence of grass margins had a significant positive effect on the abundance of grassland generalist moths ($P = 0.046$, Table A12, Fig. A8). Grassland restoration had a greater positive effect on the abundance of grassland generalist moths than the creation of grass margins (Fig. A8). However, the difference in effect of the two intervention

types was non-significant: The parameter for the interaction between the variables "presence of AES" and "type of AES" for grassland generalists was positive but did not differ significantly from zero ($P = 0.242$, Table A12, Fig. A8). This increased positive effect of grassland restoration compared to creation of grass margins was significantly greater for CG species ($P < 0.001$, Table A12, Fig. A8), but non-significantly lower for other species ($P = 0.816$). Thus for CG moths, but not grassland generalist moths or other moths, grassland restoration leads to a significantly greater increase in abundance than the creation of grass margins.

Discussion

I found that for moth species associated with CG habitat, increases in abundance were greater following grassland restoration than they were following the creation of grass margins. To my knowledge, this is the first analysis to directly compare the effects of these two AES intervention types on the abundance of insect groups. One previous study did find significant positive effects of AES-managed species-rich grasslands, but not grass margins, on the abundance of macro-moths (Fuentes-Montemayor, Goulson & Park 2011). However, the authors of that study included the AES-managed species-rich grassland which had been restored from improved grassland – not just arable fields. On the other hand, here I investigated two AES interventions that both apply to arable land, thus I can offer exclusive advice to land managers involved with insect conservation on arable farms: Assuming equal costs per unit area of the two AES interventions, I propose restoring arable fields to species-rich grassland instead of creating grass margins to maximise increases in insect biodiversity on arable fields.

However, land managers considering this advice should also consider the following issues: firstly, the cost per area for the two interventions is probably not equal. In 2014, farmers in England were compensated £280 per hectare to revert arable fields to species-rich grassland, £340 per hectare to create generic grass margins and £450 per hectare to create grass margins sown with nectar-rich wildflowers (NE 2013). This implies that of the two AES interventions considered in this analysis, the option which leads to greatest increases in the abundance of moths is also the cheapest. On the other

hand, arable field margins may be preferred areas for AES habitat creation as they have lower crop yields than arable field centres (Pywell *et al.* 2015). Secondly, the moth surveys in this study used light traps, which can attract individuals from >30m away (Merckx & Slade 2014). In 2014 some moth individuals were probably attracted to light traps from outside of grass margins, which only comprise small strips of grassland habitat. Clearly my observations of moth abundance on and around grass margins might be conservative indicators of moth density within the grass margin. Future studies might use spatially explicit survey techniques to better understand the biodiversity benefits of AES interventions per unit area.

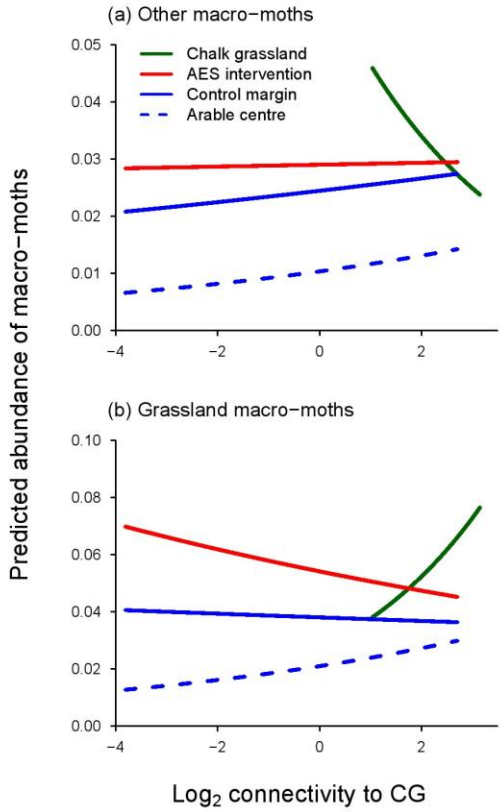


Figure A1

Model-fitted abundance of (a) "other" macro-moths (141 species) and (b) grassland associated macro-moths (24 species) across a range of connectivity to CG on each of four land management types: CG, AES interventions, control margins and arable field centres. See Appendix A3 for criteria used to determine species specialism. A high value of connectivity to CG means that a site was closer to larger areas of CG habitat (Appendix A2). Connectivity to CG of zero represents the mean connectivity to CG of macro-moth survey locations in this study. Predictions were produced using the generalised linear mixed model (GLMM) detailed in Table 1, using the range of connectivity to CG that was observed for each management type. Unlike for CG species, the slope with connectivity on AES interventions (solid red) was not significantly different from the slope on control margins (solid blue) for both grassland and other species (Table 1).

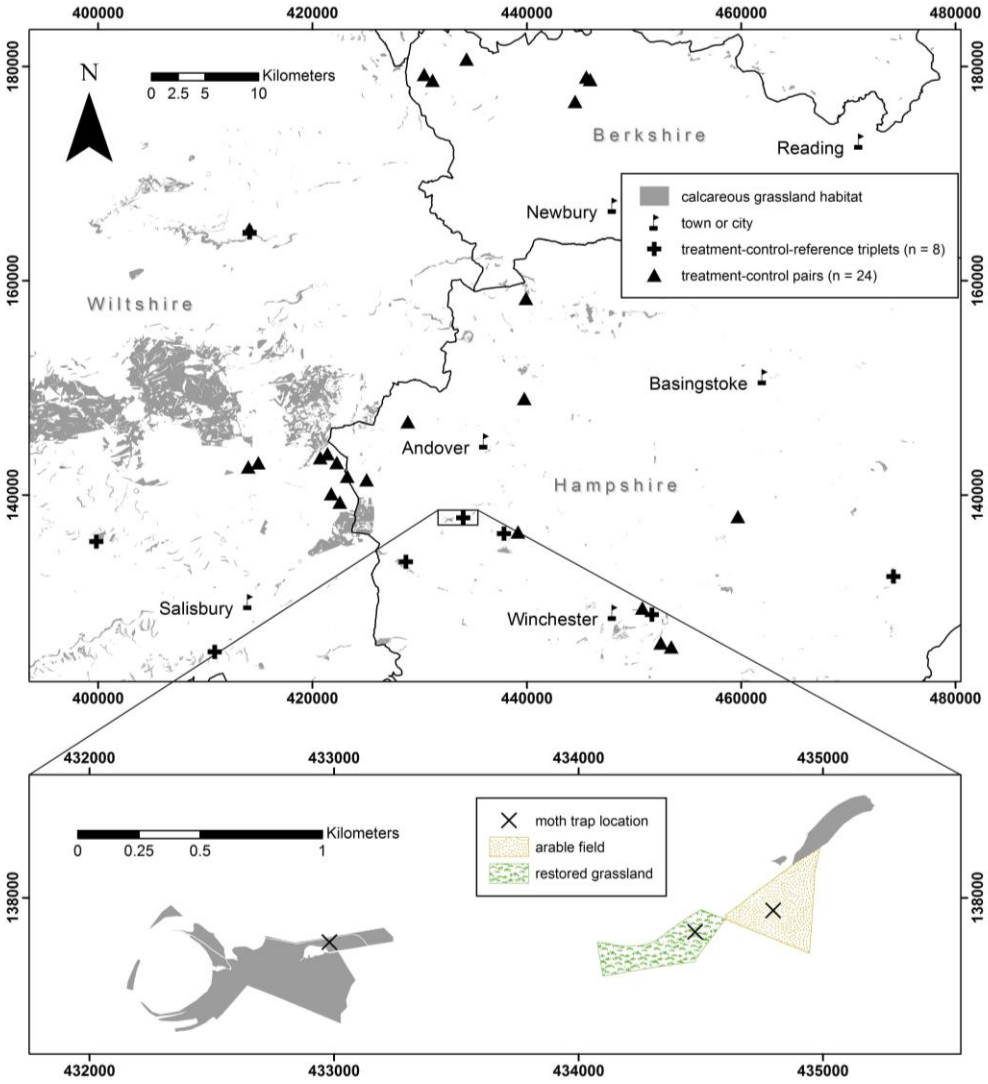
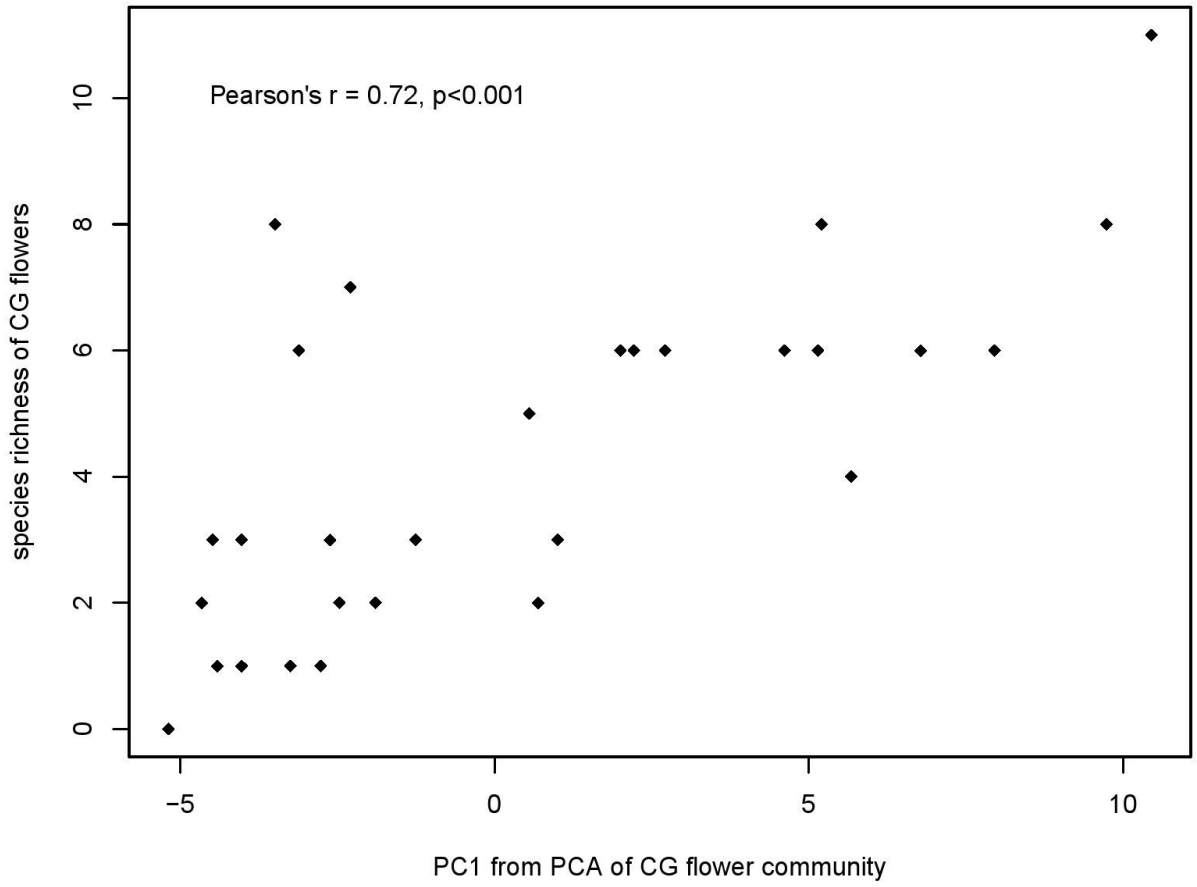


Figure A2

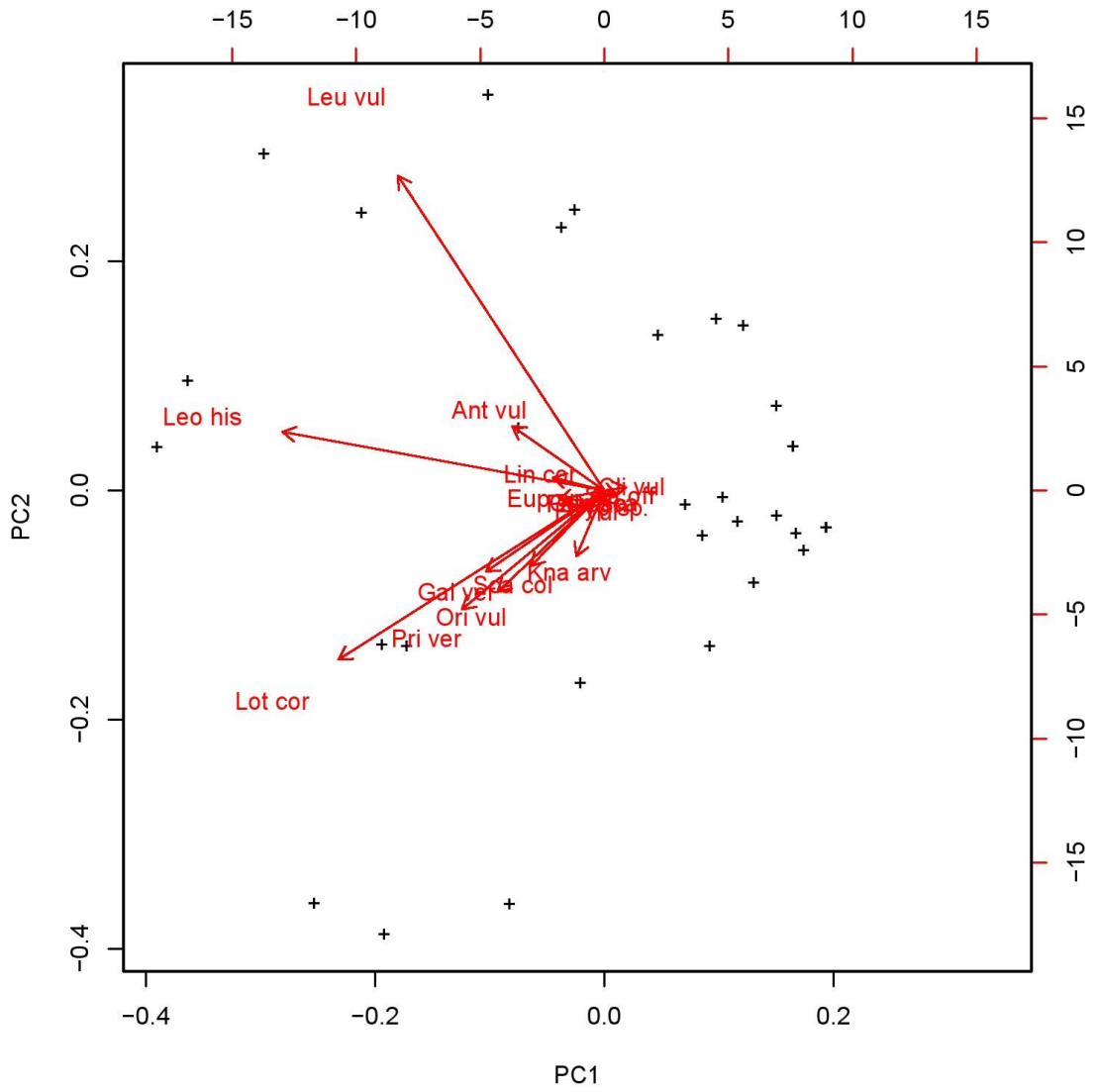
(Top) Pairs and triplets of moth survey sites located at a range of distances from calcareous grassland (CG, grey polygons) across Hampshire, Wiltshire and Berkshire, central-southern England. Treatment-control pairs comprise a restored grassland and an arable field of similar size <1km away from each other. Treatment-control-reference triplets also include a semi-natural CG site within 3km. (bottom) Close-up of the three moth survey locations in a treatment-control-reference triplet. Coverage of CG habitat was obtained from local data centres and Natural England (HBIC 2014; NE 2014b; TVERC 2015; WSBRC 2015). All-numeric coordinates from Great Britain's Ordnance Survey (OS) National Grid are displayed. The latitude and longitude at the centre of this map is approximately 51°29′10″N 01°50′62″W. Contains information from OS licensed under the Open Government License v3.0.



3489

3490 **Figure A3**

3491 Scatterplot of the relationship between the "CG flowers" variable, which is the first
3492 principle component from a PCA of the calcareous grassland (CG) wildflower
3493 community, and the observed species richness of CG flowers across restored grassland
3494 fields. Results of a Pearson's correlation between the two variables are displayed.



3495

3496 **Figure A4**

3497 Loadings of the frequency of different CG flower species (red text and arrows) on the
3498 first two axes of a principal components analysis performed using the *prcomp* function
3499 in *R* (R Core Team 2017). Species names are shortened to the first three letters of the
3500 genus and species following nomenclature in Stace *et al.* (2010). Also shown are the
3501 component scores of each restored grassland field that was surveyed (black '+') along
3502 the two axes. The first and second principal components summarized 37.3% and 23.4%
3503 of the variation in frequency of CG flowers.

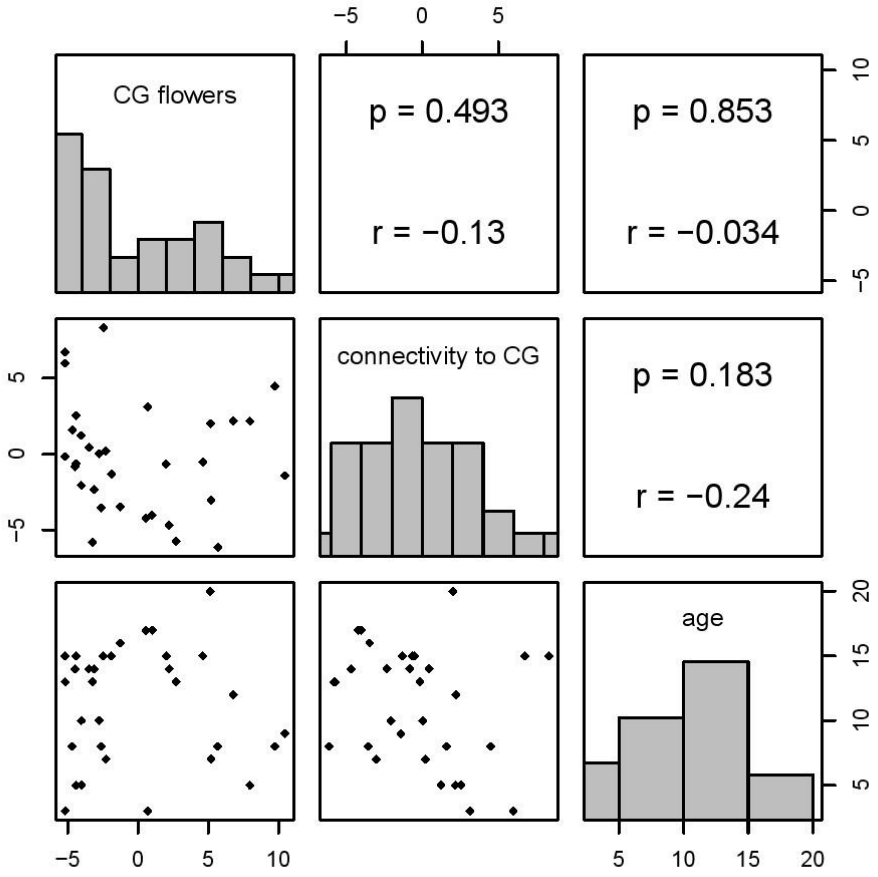


Figure A5

Correlation matrix for three key predictor variables across 32 restored grassland fields. See section *2.4. Analysis of moth abundance* of the main paper for explanations of these variables. Scatter plots on the bottom left show pairwise relationships between variables. For example, the centre-left scatterplot has CG flowers on the x-axis and connectivity to CG on the y-axis. At the top-right are the Pearson's *r* and *P*-values from Pearson's correlation tests between two variables. For example the Pearson's *r* between CG flowers and connectivity to CG across 32 fields is -0.13. Histograms of the distribution of each variable across the 32 fields are displayed on the diagonal (scale not given on histograms – y-axis values only correspond to scatter plots).

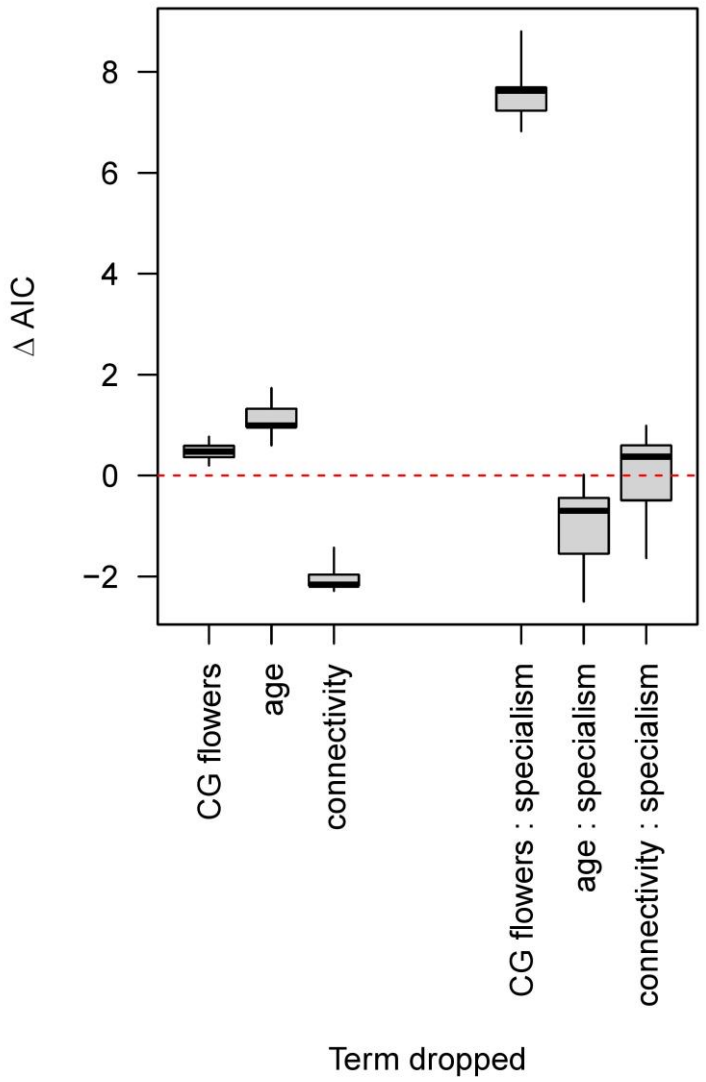
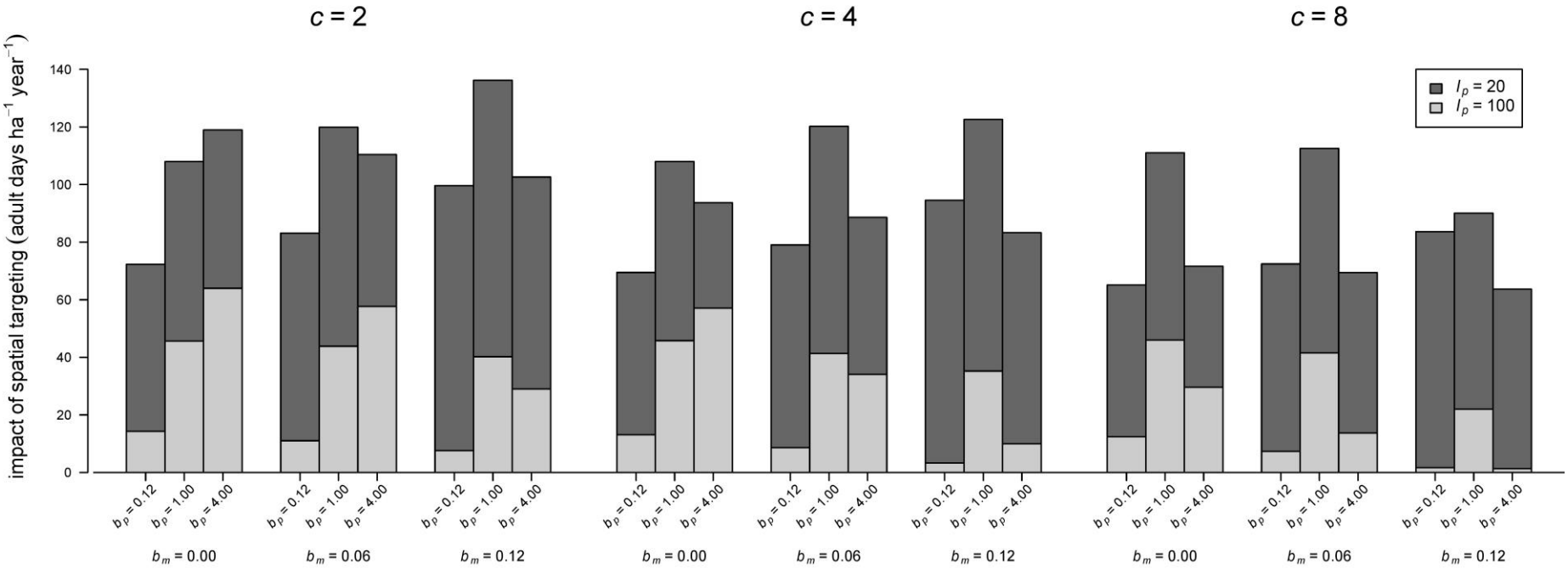


Figure A6

Boxplots of ΔAIC after dropping one of six model terms from all possible models that (1) contained that term, (2) did not contain a higher interaction for that term and (3) did contain a lower term for species specialism (N=9 models for each boxplot). Thick dark lines represent medians, boxes represent upper and lower quartiles, and whiskers represent the range. To clarify, taking all models that contained a term for "age" and "specialism" (but no higher interaction with "age") and dropping that term from each of those models would result in a median ΔAIC of 0.99; the inclusion of "age" was associated with a slight increase in parsimony.



3525

3526 **Figure A7**

3527 The impact of spatial targeting is shown for all 54 hypothetical species simulated in this study. Different coloured bars are not stacked;
3528 dark grey bars are situated behind light grey bars to use space efficiently. The impact of spatial targeting (Y-axis) represents the
3529 difference in absolute benefit between habitat patches that are as close as possible to the source population and patches that are
3530 infinitely far away. The species shown differ in their egg-laying rate in patches ($b_{p,}$ X-axis, smallest division), their egg-laying rate in
3531 the matrix (b_m, X-axis, higher division, clusters of 3 bars), their coverage of patches (c, X-axis, highest division, clusters of nine bars,
3532 see headings above bars), and mean step length in patches (dark grey bars l_p = 20, light grey bars l_p = 100).

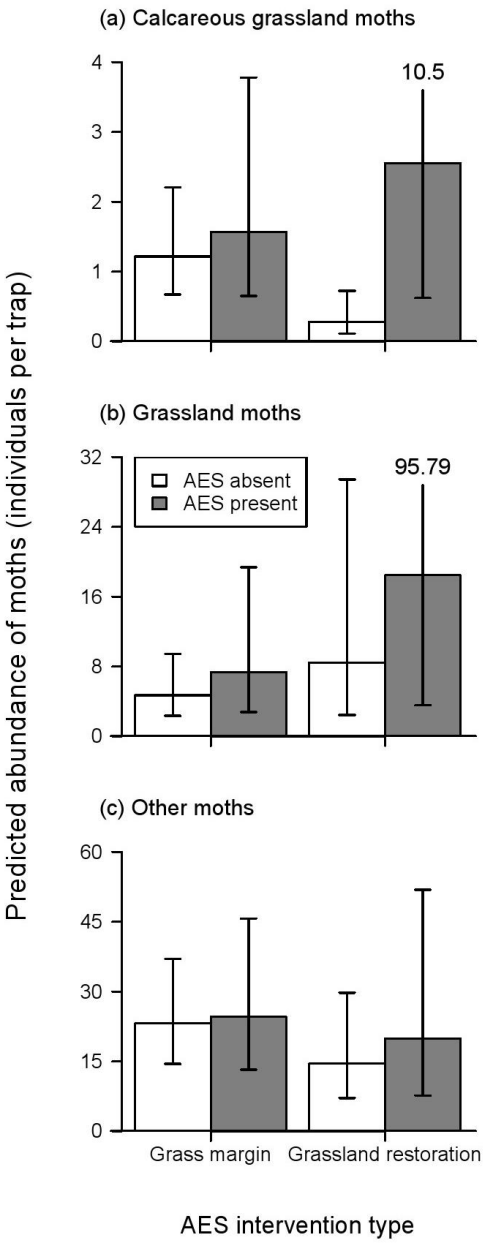


Figure A8

Predicted abundance (± 95% confidence intervals) of moths in three habitat specialism groups on sites with or without two types of agri-environment scheme (AES) intervention. Predictions were made for (a) calcareous grassland (CG) moths, (b) grassland moths and (c) moths not strongly associated with grassland (other moths). The two types of AES intervention were grass margins and arable fields restored to species-rich grassland (grey bars), and corresponding sites without interventions comprised cultivated arable margins and arable field centres (white bars). Predicted abundances and confidence intervals were calculated based on the generalised linear mixed model presented in Table A12.

Table A1

Details of the two agri-environment scheme intervention types surveyed (NE 2012). 6m buffer strips were surveyed in landscapes a, c & d, whilst nectar flower mixes were surveyed in landscape b (locations of landscapes in Fig. 3).

Option Code	Option name	Payment (£/ha)	Width	Establishment	Cutting	Further management
EE3	6m buffer strips	340	6m	Natural regeneration or sowing of grasses.	Annually cut the 3m closest to the crop.	Do not apply fertiliser. Where necessary, apply targeted herbicides.
EF4	Nectar flower mix	450	>6m	Sowing a mixture containing at least four nectar rich plant species.	Cut half the strip to 20cm in Summer. Cut entire strip to 10cm in Autumn.	Do not apply pesticides or fertilisers. Where necessary, re-establish the mixture or apply targeted herbicides.

Table A2

Total number of individuals in three groups of macro-moths trapped on five land management types in Hampshire. Traps were placed on protected calcareous grassland (CG), arable field centres, and arable field margins with or without agri-environment scheme (AES) interventions.

Management type	No. traps placed	No. other macro-moth individuals	No. grassland macro-moth individuals	No. CG macro-moth individuals
Arable field centre (near control margin)	48	586	106	24
Arable field centre (near AES intervention)	48	539	112	38
Control margin	48	1322	214	68
AES intervention	48	1444	330	89
Calcareous grassland	48	1626	386	344
Total	240	5517	1148	563

Table A3

Summary of fixed effect parameters from a generalised linear mixed model with a Poisson error structure (log link) produced using the package *lme4* (Bates *et al.* 2014). Management type was used to predict the abundance of 180 species of macro-moths in the form of the categorical variable $management_{AES}$ (4 levels: calcareous grassland, AES intervention (base level), control margin, arable centre). Random intercepts were included for field, dates of survey, and species identity nested within landscape. Observation-level random intercepts were also included to account for overdispersion in count data. Wald *Z*-tests were used to determine if parameters differed significantly from zero.

Effect	Coefficient	Std. error	*Z*	*P*(>|*Z*|)
Intercept (AES intervention)	-3.536	0.154	-22.956	<0.001
Arable centre	-1.069	0.085	-12.539	<0.001
Control margin	-0.210	0.088	-2.391	0.017
Calcareous grassland	0.272	0.127	2.134	0.033

Table A4

The distribution of four land management types across four bands of connectivity to calcareous grassland (CG) in Hampshire, UK. The four connectivity bands were defined after connectivity to CG (as calculated in Appendix A2) had been $\log_2$ transformed and centred on the mean connectivity of survey locations. The areas of agri-environment scheme (AES) interventions and control margins are shown under their existing distributions, and then under a hypothetical scenario in which AES interventions are targeted towards CG habitat. In the "targeted" scenario, AES interventions displace control margins in the highest connectivity bands, whilst the opposite happens in the lowest connectivity bands.

Connectivity band	CG habitat (km^2)	Arable centre (km^2)	AES intervention (km^2)		Control margin (km^2)		All types (km^2)
			Existing	Targeted	Existing	Targeted	
$C \geq 2$ (high)	16.40	19.01	0.14	2.24	2.10	0.00	37.65
$0 \leq C < 2$	6.46	103.47	1.46	12.19	10.72	0.00	122.12
$-2 \leq C < 0$	0.99	178.55	2.87	0.75	18.16	20.28	200.57
$C < -2$ (low)	0.15	975.39	10.70	0.00	104.17	114.87	1090.41
Total	24.00	1276.42	15.17	15.17	135.15	135.15	1450.74

Table A5

Full list of generalised linear mixed models (GLMMs, Poisson error, log-link) produced to predict the abundance of 180 species of macro-moths. Fixed effects were allowed for "species specialism" (Spe), "management" (M) and "connectivity to CG" (Con) allowing all possible interactions. Species specialism was a factor with three levels (CG species, grassland species, other species). Management was present in models in as one of three incompletely crossed factors: "management$_{full}$" (M_{full}, 5 levels: CG, AES intervention, control margin, arable field centre near AES intervention, arable centre near control margin), "management$_{AES}$" (M_{AES}, 4 levels: CG, AES intervention, control margin, arable centre) and "managment$_{margin}$" (M_{mar}, 3 levels: CG, arable margin, arable centre). Connectivity to CG was a continuous variable. Random intercepts were included for field, dates of survey, and species identity nested within landscape. Observation-level random intercepts were included to account for overdispersion in count data. Models were produced using the package *lme4* (Bates *et al.* 2014) and compiled for the table below using the package *MuMIn* (Barton 2014). Models are ranked in ascending order of AIC, with "+" indicating the inclusion of a variable in a given model. "Npar" indicates the number of parameters in that model. All models with $\Delta AIC \leq 6$ (except those with a higher AIC than any simpler nested version) are shown in bold.

Rank	(Int)	Spe	Con	Spe: Con	M_{full}	M_{full}: Spe	M_{full}: Con	M_{full}: Spe: Con	M_{AES}	M_{AES}: Spe	M_{AES}: Con	M_{AES}: Spe: Con	M_{mar}	M_{mar}: Spe	M_{mar}: Con	M_{mar}: Spe: Con	Npar	Log-likelihood	AIC	ΔAIC
1	**+**	**+**	**+**	**+**					**+**	**+**	**+**	**+**					**28**	**-6521.29**	**13098.69**	**0.00**
2	**+**	**+**	**+**	**+**									**+**	**+**	**+**	**+**	**22**	**-6528.37**	**13100.81**	**2.13**
3	+	+	+	+	+	+	+	+									34	-6519.69	13107.54	8.85
4	+	+	+	+					+		+						16	-6546.05	13124.14	25.45
5	+	+	+	+					+	+	+						22	-6540.61	13125.28	26.60
6	+	+	+	+									+	+	+		18	-6544.75	13125.54	26.86
7	+	+	+	+									+		+		14	-6549.45	13126.92	28.23
8	+	+	+	+	+		+										18	-6545.71	13127.47	28.78
9	+	+	+	+	+	+	+										26	-6539.82	13131.74	33.05
10	+	+	+	+					+								13	-6554.13	13134.28	35.59
11	+	+	+	+	+												14	-6554.01	13136.06	37.37
12	+	+	+	+					+	+							19	-6549.10	13136.26	37.57
13	+	+	+	+									+	+			16	-6552.54	13137.11	38.42
14	+	+	+	+									+				12	-6556.80	13137.63	38.94
15	+	+	+	+	+	+											22	-6548.55	13141.17	42.48
16	+	+	+						+	+	+						20	-6554.26	13148.57	49.89
17	+	+	+										+	+	+		16	-6558.30	13148.64	49.95
18	+	+	+		+	+	+										24	-6553.17	13154.43	55.75
19	+	+	+						+	+							17	-6562.19	13158.43	59.74
20	+	+	+										+	+			14	-6565.51	13159.06	60.37
21	+	+							+	+							16	-6563.98	13160.00	61.32

Rank	(Int)	Spe	Con	Spe: Con	M_{full}	M_{full}: Spe	M_{full}: Con	M_{full}: Spe: Con	M_{AES}	M_{AES}: Spe	M_{AES}: Con	M_{AES}: Spe: Con	M_{mar}	M_{mar}: Spe	M_{mar}: Con	M_{mar}: Spe: Con	Npar	Log-likelihood	AIC	ΔAIC
22	+	+											+	+			13	-6567.44	13160.91	62.23
23	+	+	+		+	+											20	-6561.33	13162.71	64.02
24	+	+			+	+											19	-6563.17	13164.40	65.71
25	+		+						+		+						12	-6594.14	13212.31	113.62
26	+	+	+						+		+						14	-6592.51	13213.04	114.36
27	+		+										+		+		10	-6597.56	13215.14	116.45
28	+		+		+		+										14	-6593.80	13215.64	116.95
29	+	+	+										+		+		12	-6595.92	13215.86	117.18
30	+	+	+		+		+										16	-6592.17	13216.37	117.69
31	+		+						+								9	-6601.50	13221.02	122.33
32	+	+	+						+								11	-6599.85	13221.72	123.03
33	+								+								8	-6603.20	13222.41	123.72
34	+		+		+												10	-6601.38	13222.77	124.08
35	+	+							+								10	-6601.55	13223.12	124.43
36	+	+	+		+												12	-6599.74	13223.50	124.81
37	+				+												9	-6603.15	13224.30	125.62
38	+		+										+				8	-6604.21	13224.43	125.74
39	+	+			+												11	-6601.50	13225.01	126.32
40	+	+	+										+				10	-6602.54	13225.10	126.42
41	+												+				7	-6606.05	13226.12	127.43
42	+	+											+				9	-6604.40	13226.82	128.13
43	+	+	+	+													10	-6630.80	13281.62	182.93
44	+		+														6	-6677.65	13367.31	268.63
45	+	+	+														8	-6675.92	13367.86	269.17
46	+																5	-6686.76	13383.53	284.84
47	+	+															7	-6685.02	13384.05	285.36

3578

Table A6

Full list of scientific names (following Agassiz, Beavan & Heckford 2013) of all 180 macro-moth species caught in the study. Shown are the habitat specialism group each species fell into (oth = other species, gra = grassland species, cgr = calcareous grassland species, see Appendix A3 for classification details), as well as the number of individuals trapped on each distinct land management type. Twice as many trapping events occurred on arable field centres than on each other land management type, so I provide an appropriate comparison by displaying the number of individuals on arable field centres divided by two (in brackets).

Species name	Habitat specialism	Individuals on arable centres (96 traps)	Individuals on arable centres divided by 2	Individuals on control margins (48 traps)	Individuals on AES intervention (48 traps)	Individuals on calc. grassland (48 traps)	Total
Abraxas grossulariata	oth	0	(0)	1	0	0	1
Acronicta leporina	oth	0	(0)	0	1	1	2
Acronicta psi agg.	oth	2	(1)	4	8	0	14
Acronicta rumicis	oth	2	(1)	2	4	2	10
Agrotis puta	oth	1	(0.5)	2	3	5	11
Agrotis segetum	oth	2	(1)	1	0	0	3
Alcis repandata	oth	0	(0)	6	8	2	16
Amphipyra pyramidea agg.	oth	0	(0)	0	1	1	2
Amphipyra tragopoginis	oth	9	(4.5)	3	7	11	30
Apamea epomidion	oth	3	(1.5)	6	3	4	16
Apamea monoglypha	oth	327	(163.5)	260	222	298	1107
Apamea remissa	oth	1	(0.5)	0	5	7	13
Apamea unanimis	oth	1	(0.5)	0	5	0	6
Apeira syringaria	oth	0	(0)	1	0	0	1
Apoda limacodes	oth	2	(1)	1	1	0	4
Arctia caja	oth	10	(5)	9	8	2	29
Autographa gamma	oth	1	(0.5)	0	3	2	6
Autographa jota	oth	1	(0.5)	3	5	3	12
Autographa pulchrina	oth	0	(0)	1	0	0	1
Biston betularia	oth	2	(1)	3	4	1	10
Cabera pusaria	oth	0	(0)	3	0	0	3
Calliteara pudibunda	oth	4	(2)	3	2	1	10
Campaea margaritaria	oth	0	(0)	2	2	2	6
Caradrina morpheus	oth	6	(3)	11	9	7	33
Ceramica pisi	oth	0	(0)	0	1	0	1
Charanyca trigrammica	oth	7	(3.5)	5	7	10	29
Chloroclystis v-ata	oth	0	(0)	2	1	4	7
Cilix glaucata	oth	2	(1)	0	1	3	6
Cleorodes lichenaria	oth	0	(0)	1	1	1	3
Colocasia coryli	oth	3	(1.5)	1	2	4	10
Cosmia trapezina	oth	0	(0)	1	1	4	6
Cosmorhoe ocellata	oth	0	(0)	0	0	1	1
Craniophora ligustri	oth	3	(1.5)	6	5	9	23
Crocallis elinguaria	oth	0	(0)	1	1	0	2
Cybosia mesomella	oth	0	(0)	3	5	1	9
Deltote pygarga	oth	1	(0.5)	1	2	0	4
Diachrysia chrysitis	oth	5	(2.5)	7	13	8	33
Diarsia mendica	oth	5	(2.5)	9	7	8	29
Diarsia rubi	oth	20	(10)	17	18	20	75
Drepana falcataria	oth	1	(0.5)	0	0	0	1
Dysstroma truncata	oth	0	(0)	4	2	7	13
Ectropis crepuscularia	oth	5	(2.5)	4	2	3	14
Eilema complana	oth	4	(2)	5	6	55	70
Eilema griseola	oth	16	(8)	56	36	24	132
Eilema lurideola	oth	130	(65)	268	260	144	802
Eilema sororcula	oth	0	(0)	1	0	2	3
Electrophaes corylata	oth	0	(0)	0	0	1	1
Epirrhoe alternata	oth	1	(0.5)	7	4	3	15
Eupithecia absinthiata	oth	1	(0.5)	0	0	0	1
Eupithecia centaureata	oth	0	(0)	2	0	3	5

Species name	Habitat specialism	Individuals on arable centres (96 traps)	Individuals on arable centres divided by 2	Individuals on control margins (48 traps)	Individuals on AES intervention (48 traps)	Individuals on calc. grassland (48 traps)	Total
Eupithecia haworthiata	oth	2	(1)	4	7	11	24
Eupithecia tripunctaria	oth	0	(0)	0	1	0	1
Euplexia lucipara	oth	1	(0.5)	0	0	0	1
Euproctis similis	oth	5	(2.5)	8	13	8	34
Euthrix potatoria	oth	14	(7)	6	18	7	45
Furcula furcular	oth	0	(0)	1	1	0	2
Gandaritis pyraliata	oth	3	(1.5)	3	4	0	10
Gastropacha quercifolia	oth	2	(1)	2	2	0	6
Geometra papilionaria	oth	0	(0)	1	0	1	2
Habrosyne pyritoides	oth	7	(3.5)	0	2	2	11
Hada plebeja	oth	4	(2)	1	7	41	53
Hadena bicruris	oth	0	(0)	1	1	0	2
Hemistola chrysoprasaria	oth	0	(0)	0	1	0	1
Hemithea aestivaria	oth	0	(0)	0	1	0	1
Herminia grisealis	oth	2	(1)	1	1	1	5
Herminia tarsipennalis	oth	2	(1)	4	0	0	6
Hoplodrina octogeneria/blanda	oth	47	(23.5)	54	75	108	284
Horisme tersata	oth	1	(0.5)	2	2	3	8
Horisme vitalbata	oth	2	(1)	3	4	10	19
Hydriomena furcata	oth	1	(0.5)	0	0	0	1
Hydriomena impluviata	oth	1	(0.5)	0	0	0	1
Hypena proboscidalis	oth	1	(0.5)	10	4	0	15
Idaea aversata	oth	1	(0.5)	13	8	11	33
Idaea biselata	oth	2	(1)	3	4	3	12
Idaea dimidiate	oth	1	(0.5)	1	2	2	6
Lacanobia oleracea	oth	2	(1)	6	6	3	17
Lacanobia w-latinum	oth	0	(0)	1	1	1	3
Laothoe populi	oth	3	(1.5)	7	5	5	20
Laspeyria flexula	oth	0	(0)	2	0	1	3
Leucania comma	oth	10	(5)	6	1	7	24
Leucoma salicis	oth	0	(0)	1	0	0	1
Ligdia adustata	oth	0	(0)	3	1	1	5
Lomaspilis marginata	oth	0	(0)	1	2	0	3
Lomographa temerata	oth	1	(0.5)	1	1	12	15
Macaria liturata	oth	0	(0)	0	0	1	1
Mamestra brassicae	oth	1	(0.5)	0	0	0	1
Melanchra persicariae	oth	4	(2)	10	25	22	61
Melanthia procellata	oth	0	(0)	0	2	0	2
Mesapamea secalis agg.	oth	56	(28)	143	203	101	503
Miltochrista miniata	oth	2	(1)	9	6	6	23
Mimas tiliae	oth	0	(0)	0	1	0	1
Mythimna albipuncta	oth	2	(1)	1	0	2	5
Mythimna ferrago	oth	16	(8)	18	38	44	116
Noctua comes	oth	3	(1.5)	6	7	3	19
Noctua fimbriata	oth	8	(4)	2	2	3	15
Noctua interjecta	oth	0	(0)	1	0	0	1
Noctua janthe	oth	3	(1.5)	1	2	2	8
Noctua orbona	oth	0	(0)	0	0	1	1
Noctua pronuba	oth	135	(67.5)	51	68	187	441
Nola cucullatella	oth	0	(0)	0	0	1	1
Notodonta dromedarius	oth	0	(0)	1	0	0	1
Notodonta ziczac	oth	0	(0)	0	0	1	1
Nudaria mundana	oth	2	(1)	2	10	2	16
Ochropacha duplaris	oth	0	(0)	1	1	0	2
Ochropleura plecta	oth	12	(6)	17	19	57	105
Opisthograptis luteolata	oth	1	(0.5)	1	2	0	4
Ourapteryx sambucaria	oth	0	(0)	1	1	0	2
Pasiphila chloerata	oth	0	(0)	0	0	1	1
Pasiphila rectangulata	oth	0	(0)	0	0	2	2
Peribatodes rhomboidaria	oth	2	(1)	7	3	6	18
Phalera bucephala	oth	3	(1.5)	4	4	9	20
Philereme transversata	oth	1	(0.5)	0	2	2	5
Phlogophora meticulosa	oth	1	(0.5)	0	0	2	3
Photedes fluxa	oth	0	(0)	1	0	0	1

Species name	Habitat specialism	Individuals on arable centres (96 traps)	Individuals on arable centres divided by 2	Individuals on control margins (48 traps)	Individuals on AES intervention (48 traps)	Individuals on calc. grassland (48 traps)	Total
Phragmatobia fuliginosa	oth	65	(32.5)	27	49	110	251
Plagodis dolabraria	oth	1	(0.5)	2	0	0	3
Polia nebulosi	oth	2	(1)	3	3	2	10
Pseudoips prasinana	oth	0	(0)	0	1	4	5
Ptilodon capucina	oth	1	(0.5)	0	0	0	1
Ptilodon cucullina	oth	1	(0.5)	0	0	0	1
Rhodometra sacraria	oth	1	(0.5)	0	0	0	1
Rusina ferruginea	oth	6	(3)	10	10	17	43
Scopula imitaria	oth	0	(0)	0	1	0	1
Selenia dentaria	oth	0	(0)	1	1	0	2
Sideridis rivularis	oth	0	(0)	0	2	0	2
Smerinthus ocellata	oth	0	(0)	1	0	0	1
Sphinx ligustri	oth	8	(4)	9	11	22	50
Sphinx pinastri	oth	1	(0.5)	0	2	0	3
Spilosoma lubricipeda	oth	8	(4)	25	11	14	58
Spilosoma lutea	oth	33	(16.5)	31	41	11	116
Stauropus fagi	oth	0	(0)	0	0	6	6
Subacronicta megacephala	oth	0	(0)	0	1	1	2
Thyatira batis	oth	0	(0)	1	0	0	1
Triphosa dubitata	oth	1	(0.5)	0	0	0	1
Xanthorhoe ferrugata	oth	2	(1)	1	1	1	5
Xanthorhoe fluctuate	oth	1	(0.5)	0	1	2	4
Xanthorhoe montanata	oth	1	(0.5)	2	1	1	5
Xanthorhoe quadrifasiata	oth	1	(0.5)	0	0	0	1
Xanthorhoe spadicearia	oth	0	(0)	2	0	2	4
Xestia c-nigrum	oth	22	(11)	33	26	43	124
Xestia Triangulum	oth	25	(12.5)	28	35	33	121
Abrostola tripartite	gra	2	(1)	2	5	0	9
Agrotis exclamationis	gra	38	(19)	50	52	51	191
Apamea crenata	gra	1	(0.5)	0	0	0	1
Apamea sordens	gra	17	(8.5)	13	8	9	47
Aplocera plagiata	gra	0	(0)	1	0	0	1
Axylia putris	gra	24	(12)	27	32	35	118
Caradrina clavipalpis	gra	1	(0.5)	10	1	2	14
Cerapteryx graminis	gra	0	(0)	0	0	1	1
Deilephila elpenor	gra	5	(2.5)	3	5	6	19
Ecliptopera silaceata	gra	0	(0)	0	0	2	2
Hepialus humuli	gra	0	(0)	0	0	2	2
Korscheltellus lupulina	gra	17	(8.5)	23	89	169	298
Lasiocampa quercus	gra	0	(0)	0	1	1	2
Luperina testacea	gra	4	(2)	0	1	0	5
Macrothylacia rubi	gra	0	(0)	0	1	1	2
Mythimna conigera	gra	2	(1)	2	1	3	8
Mythimna impure	gra	30	(15)	35	76	39	180
Mythimna pallens	gra	45	(22.5)	25	20	18	108
Oligia fasciuncula	gra	3	(1.5)	1	3	4	11
Oligia strigilis	gra	27	(13.5)	20	32	40	119
Rivula sericealis	gra	1	(0.5)	1	1	1	4
Scotopteryx chenopodiata	gra	0	(0)	0	1	0	1
Triodia sylvina	gra	0	(0)	0	0	1	1
Tyria jacobaeae	gra	1	(0.5)	1	1	1	4
Agrotis clavis	cgr	7	(3.5)	11	8	11	37
Apamea anceps	cgr	0	(0)	0	1	0	1
Apamea lithoxylaea	cgr	1	(0.5)	5	6	7	19
Apamea sublustris	cgr	16	(8)	5	9	111	141
Catarhoe cuculata	cgr	0	(0)	0	0	2	2
Catarhoe rubidata	cgr	0	(0)	0	0	1	1
Cucullia umbratica	cgr	0	(0)	0	0	2	2
Deilephila porcellus	cgr	20	(10)	18	20	103	161
Eremobia ochroleuca	cgr	13	(6.5)	17	34	79	143
Hadena confuse	cgr	0	(0)	0	0	2	2
Hecatera bicolorata	cgr	0	(0)	0	1	3	4
Idaea fuscovenosa	cgr	0	(0)	0	0	1	1
Litoligia literosa	cgr	1	(0.5)	3	4	21	29

Species name	Habitat specialism	Individuals on arable centres (96 traps)	Individuals on arable centres divided by 2	Individuals on control margins (48 traps)	Individuals on AES intervention (48 traps)	Individuals on calc. grassland (48 traps)	Total
Lygephila pastinum	cgr	0	(0)	0	0	1	1
Mesoligia furuncula	cgr	4	(2)	9	6	0	19

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Table A7

Summary of fixed effect parameters in the lowest AIC model predicting the abundance of 180 species of macro-moths (parameters = 30, Log Likelihood = -6534.0, AIC = 13124.00, ΔAIC next best = 1.58). This generalised linear mixed model (GLMM, negative binomial error, log-link) included a three way interaction between the variables managementAES (4 levels: calcareous grassland (CG), AES intervention (base level), control margin, arable centre), species specialism (3 levels: CG species, grassland species (base level), or other species) and connectivity to CG. Random intercepts were included for field, dates of survey, and species identity nested within landscape. Models were produced using the package glmmADMB (Skaug *et al.* 2015) using Wald Z-tests to determine if parameters differed significantly from zero (parameters with P < 0.05 in bold).

Species group	Parameter	Par. estimate	Std. error	*Z*	*P*(>|*Z*|)
Grassland species	**Intercept for grassland species (on AES intervention at mean connectivity to CG)**	**-2.693**	**0.319**	**-8.450**	**<0.001**
	Arable centre	**-0.944**	**0.141**	**-6.710**	**<0.001**
(associated with grassland but not calcareous grassland)	**Control margin**	**-0.353**	**0.154**	**-2.290**	**0.022**
	Calcareous grassland	-0.769	0.436	-1.760	0.078
	Connectivity to CG	-0.076	0.066	-1.140	0.255
	Connectivity to CG: Arable centre	**0.201**	**0.073**	**2.760**	**0.006**
	Connectivity to CG: Control margin	0.055	0.083	0.660	0.508
	Connectivity to CG: Calcareous grassland	**0.446**	**0.197**	**2.270**	**0.024**
Other species	Intercept for other species (on AES intervention at mean connectivity to CG)	-0.645	0.331	-1.950	0.051
	Arable centre	-0.061	0.147	-0.410	0.680
(not associated with grassland or calcareous grassland)	Control margin	0.211	0.159	1.330	0.184
	Calcareous grassland	**1.575**	**0.350**	**4.500**	**<0.001**
	Connectivity to CG	0.081	0.063	1.300	0.193
	Connectivity to CG: Arable centre	-0.087	0.080	-1.080	0.279
	Connectivity to CG: Control margin	-0.026	0.086	-0.310	0.759
	Connectivity to CG: Calcareous grassland	**-0.765**	**0.157**	**-4.870**	**<0.001**
Calcareous grassland (CG) species	**Intercept for CG species (on AES intervention at mean connectivity to CG)**	**-1.196**	**0.515**	**-2.320**	**0.020**
	Arable centre	-0.447	0.282	-1.580	0.114
	Control margin	0.254	0.273	0.930	0.352
(associated with calcareous grassland)	Calcareous grassland	0.591	0.658	0.900	0.369
	Connectivity to CG	**0.537**	**0.132**	**4.070**	**<0.001**
	Connectivity to CG: Arable centre	0.183	0.179	1.030	0.305
	Connectivity to CG: Control margin	**-0.393**	**0.170**	**-2.310**	**0.021**
	Connectivity to CG: Calcareous grassland	-0.151	0.286	-0.530	0.598

Table A8

Details of the 32 restored grassland fields **(**treatment sites**)** in this study. Displayed are the locations of each field on the Ordnance Survey National Grid, field area, age of restoration, connectivity (see the methods section of the main article for details of calculation and transformation of this variable), establishment method (either naturally regenerated or sown with seeds of grasses and wildflowers), frequency of CG wildflowers (the negative of the first principle component shown in Fig. A4 – this variable is positively correlated with the frequency of the vast majority of CG indicator wildflower species) and species richness of indicator wildflower species.

OS Grid Reference	Area (ha)	Age of restoration (years)	Connectivity	Establishment method	Frequency of CG flowers (-PCA1)	Species richness of CG flowers
ST9935	9.56	3	6.27	Natural regen	-5.19	0
SU1025	14.87	5	2.47	Sown	7.96	6
SU1342	16.47	15	-0.24	Sown	4.62	6
SU1364	5.96	5	2.83	Sown	-4.41	1
SU1464	19.78	5	1.52	Sown	-4.02	1
SU1443	17.27	13	0.14	Sown	-5.19	0
SU2043	11.33	15	7.02	Natural regen	-5.19	0
SU2144	19.38	15	8.61	Natural regen	-2.47	2
SU2140	7.29	9	-1.11	Sown	10.45	11
SU2242	10.82	15	-0.37	Natural regen	2.00	6
SU2239	4.12	8	4.78	Sown	9.73	8
SU2341	22.66	15	-1.02	Natural regen	-1.89	2
SU2541	9.37	15	-0.33	Natural regen	-4.41	1
SU2834	18.00	8	1.87	Natural regen	-4.66	2
SU2846	5.92	17	-3.73	Sown	1.00	3
SU3079	23.62	7	-2.71	Sown	5.20	8
SU3178	34.76	16	-3.16	Sown	-1.26	3
SU3480	37.52	17	-3.92	Sown	0.55	5
SU3437	6.31	14	-0.53	Sown	-4.48	3
SU3736	7.99	14	0.74	Sown	-3.50	8
SU3936	9.76	14	-2.03	Sown	-3.11	6
SU3948	7.21	8	-3.25	Sown	-2.62	3
SU3958	2.57	3	3.41	Sown	0.69	2
SU4476	26.56	8	-5.83	Sown	5.67	4
SU4579	20.47	13	-5.43	Sown	2.72	6
SU4578	14.89	13	-5.50	Sown	-3.25	1
SU5029	7.28	12	2.49	Sown	6.78	6
SU5129	11.52	20	2.30	Sown	5.14	6
SU5226	33.14	10	0.33	Sown	-2.77	1
SU5325	12.57	10	-1.76	Sown	-4.03	3
SU5938	10.30	14	-4.38	Sown	2.22	6
SU7432	10.19	7	0.51	Sown	-2.29	7

Table A9

Full list of generalised linear mixed models (GLMMs, negative binomial error) produced to predict the abundance of moths. Fixed effects were allowed for "species specialism" (Spe), "habitat type" (Hab) and "connectivity to calcareous grassland (CG)" (Con) allowing all possible interactions. Species specialism was a factor with three levels (CG species, grassland species, other species). Habitat type was a factor with three levels (arable field, restored grassland, semi-natural CG). Connectivity to CG was a continuous variable. Random intercepts were included for field of survey and date of survey. Models were produced using the package *glmmADMB* (Skaug *et al.* 2015) and compiled for the table below using the package *MuMIn* (Barton 2014). Models are ranked in ascending order of AIC, with "+" indicating the inclusion of a variable in a given model. All models with $\Delta AIC \leq 6$ (except those with a higher AIC than any simpler nested version) are shown in bold.

Rank	(Int)	Spe	Con	Spe:Con	Hab	Spe:Hab	Con:Hab	Spe:Con:Hab	Log-likelihood	AIC	ΔAIC
1	**+**	**+**	**+**	**+**	**+**	**+**			**-1536.37**	**3103.93**	**0.00**
2	**+**	**+**			**+**	**+**			**-1541.21**	**3107.19**	**3.26**
3	+	+	+	+	+	+	+		-1536.35	3108.22	4.29
4	+	+	+		+	+			-1541.21	3109.32	5.39
5	+	+	+	+	+	+	+	+	-1534.58	3113.48	9.55
6	+	+	+		+	+	+		-1541.19	3113.57	9.64
7	+	+	+	+	+				-1560.53	3143.71	39.78
8	+	+			+				-1565.00	3146.35	42.42
9	+	+	+	+	+		+		-1560.47	3147.84	43.91
10	+	+	+		+				-1565.00	3148.44	44.51
11	+	+	+		+		+		-1564.78	3152.21	48.28
12	+	+	+	+					-1589.18	3196.80	92.87
13	+	+							-1594.81	3201.82	97.90
14	+	+	+						-1593.94	3202.15	98.22
15	+				+				-1697.94	3408.08	304.16
16	+		+		+				-1697.83	3409.93	306.00
17	+		+		+		+		-1697.41	3413.26	309.33
18	+		+						-1723.85	3457.84	353.92
19	+								-1725.10	3458.30	354.37

Table A10

Summary of fixed effect parameters in the lowest AIC model predicting the presence of moths species in three habitat specialism groups (Log Likelihood = -883.62, AIC = 1789.88). In binomial models I used the number of species in a given habitat specialism group in each trap as the number of successes, and the total number of species recorded for that habitat specialism group as the number of trials. This generalised linear mixed model (GLMM, binomial error) included an interaction between the variables habitat type (3 levels: arable field, restored grassland (base level), semi-natural CG) and species specialism (3 levels: CG species (base level), grassland species, other species). Random intercepts were included for field of survey and date of survey. During model selection there was no model with $\Delta AIC \leq 6$ and a lower AIC than any simpler nested version.

Species group	Parameter	Estimate	Std. error
Calcareous grassland (CG) species (associated with calcareous grassland)	Intercept (CG species on restored grassland)	-2.479	0.127
	Arable field	-1.256	0.178
	Calcareous grassland	0.270	0.211
Grassland species (associated with grassland but not calcareous grassland)	Grassland species (on restored grassland)	0.624	0.101
	Arable field	0.733	0.190
	Calcareous grassland	-0.173	0.231
Other species (not associated with grassland or calcareous grassland)	Other species (on restored grassland)	-0.459	0.095
	Arable field	0.995	0.183
	Calcareous grassland	0.262	0.213

Table A11

Summary of fixed effect parameters in the lowest AIC model predicting the presence of moths species in three habitat specialism groups on arable fields restored to species-rich grassland (Log Likelihood = -426.52, AIC = 863.36). In binomial models I used the number of species in a given habitat specialism group in each trap as the number of successes, and the total number of species recorded for that habitat specialism group on restored grassland fields as the number of trials. This generalised linear mixed model (GLMM, binomial error) included only species specialism as a predictor (3 levels: CG species (base level), grassland species, other species). Random intercepts were included for field of survey and date of survey. During model selection there was no model with $\Delta AIC \leq 6$ and a lower AIC than any simpler nested version.

Parameter	Estimate	Std. error
Intercept (CG species)	-2.328	0.115
Grassland species	0.576	0.101
Other species	-0.252	0.096

Table A12

Summary of fixed effect parameters in a generalised linear mixed-effects model (GLMM, negative binomial error) predicting the abundance of moths (Log Likelihood = -2021.21, AIC = 4073.16). This model included a three-way interaction between the variables species specialism (three levels: grassland species (base level), CG species, other species), presence of AES (two levels: absent (base level) or present) and type of AES (two levels: grass margin (base level) or grassland restoration). Random intercepts were included for field of survey and date of survey. Wald Z-tests were used to determine if parameters differed significantly from zero, and parameters relevant to my core hypothesis are highlighted in grey. This model had a dispersion parameter $\alpha = 1.50$, indicating that data were highly overdispersed.

Species group	Parameter	Estimate	Std. error	*Z*	*P*(>|*Z*|)
Grassland species (associated with grassland but not calcareous grassland)	Intercept (Grassland species where type of AES = grass margin and presence of AES = absent)	1.547	0.240	6.440	<0.001
	Presence of AES = present	0.445	0.223	1.997	0.046
	Type of AES = grassland restoration	0.587	0.305	1.926	0.054
	Presence of AES = present * type of AES = grassland restoration	0.336	0.287	1.171	0.242
Calcareous grassland (CG) species (associated with calcareous grassland)	CG species (where type of AES = grass margin and presence of AES = absent)	-1.351	0.230	-5.885	<0.001
	Presence of AES = present	-0.190	0.316	-0.601	0.548
	Type of AES = grassland restoration	-2.051	0.350	-5.852	<0.001
	Presence of AES = present * type of AES = grassland restoration	1.614	0.452	3.574	<0.001
Other species (not associated with grassland or calcareous grassland)	Other species (where type of AES = grass margin and presence of AES = absent)	1.595	0.191	8.346	<0.001
	Presence of AES = present	-0.386	0.265	-1.458	0.145
	Type of AES = grassland restoration	-1.052	0.255	-4.127	<0.001
	Presence of AES = present * type of AES = grassland restoration	-0.081	0.350	-0.233	0.816

Appendix P1: Rewilding and Ecosystem Services POSTnote

The following report was produced in collaboration with Dr Jonathan Wentworth during my three month internship with the Parliamentary Office of Science and Technology (POST). POST is a source of independent, balanced and accessible analysis of public policy issues related to science and technology in UK Parliament. The main outputs of POST are four page policy briefs called "POSTnotes", which summarise evidence on a subject such that it can be understood by parliamentarians. The subject of the following POSTnote was pitched in competition with several others to a panel mostly comprising members of parliament and lords (the "POST board"). It received sufficient votes to warrant publication, and I was tasked with researching and writing this POSTnote throughout my internship.

The full report can also be accessed at http://researchbriefings.parliament.uk/ResearchBriefing/Summary/POST-PN-0537.

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POSTNOTE

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Rewilding and Ecosystem Services

This POSTnote explores the consequences of increasing the role of natural processes within landscapes. Evidence from the UK and abroad suggests that rewilding can benefit both wildlife and local people, but animal reintroductions could adversely affect some land-users.

Overview

- Rewilding aims to restore natural processes that are self-regulating, reducing the need for human management of land.
- Few rewilding projects are underway, and there is limited evidence on their impacts.
- Rewilding may provide ecosystem services such as flood prevention, carbon storage and recreation. It often has low input costs, but can still benefit biodiversity.
- Some valued and protected priority habitats such as chalk grassland currently depend on agricultural practices like grazing. Rewilding may not result in such habitats.
- No government policy refers explicitly to rewilding, but it has the potential to complement existing approaches to meet commitments on habitat restoration.

What is Rewilding?

There is no single definition of rewilding, but it generally refers to reinstating natural processes that would have occurred in the absence of human activity.[1,2] These include vegetation succession, where grasslands develop into wetlands or forests, and ecological disturbances caused by disease, flooding, fire and wild herbivores (plant eaters). Initially, natural processes may be restored through human interventions such as tree planting, drainage blocking and reintroducing "keystone species"[3,4] like beavers. In the long term, self-regulating natural processes may reduce the need for human management. Rewilding can have unpredictable outcomes, but it may also represent a cost-effective way to provide ecosystem services (benefits provided by natural processes)[5] such as flood prevention.[6] Rewilding might help to reduce or offset negative impacts of intensive agriculture including: soil degradation [POSTnote 502]; greenhouse-gas emissions [POSTnotes 453 & 486]; water pollution [POSTnote 478]; insect pollinator declines [POSTnote 442] and a reduction in biodiversity (the variety of living things).[7]

This briefing outlines approaches to rewilding land across Europe, as well as the potential benefits and risks involved. Rewilding has not been referred to by the UK government, so it is put into the context of relevant policy on agriculture and biodiversity. While some advocate rewilding of the seas using no-fishing zones,[8] this is not discussed here.

Rewilding and Current Conservation Practice

UK landscapes have been managed to produce food and wood for millennia, and 70% of land is currently farmed.[9] €3bn per year is spent on environmental management of farmland across the EU.[10,11] This includes maintaining wildlife habitats on farmland such as heathland and chalk grassland, which involves traditional agricultural practices such as fire and grazing.[12,13] Rewilding involves ecological restoration (the repair of degraded ecosystems),[14] and differs from mainstream conservation in two main ways:

- Existing policies promote the conservation of specific endangered species and habitats. Rewilding focuses on restoring natural processes and dynamics, and the groups of species that emerge from this.[15]
- Existing practices use active management to increase biodiversity in nature reserves. This may involve low-intensity livestock grazing, but rewilding generally has a long term goal of reduced management by humans.[16]

Conflicting Views on Rewilding

Interest in rewilding has increased rapidly in recent years.[15] Some see rewilding as a positive vision for restoring ecosystems,[17] but others feel that it is poorly defined and may result in people being excluded from natural spaces.[18] Rewilding is generally seen as an open-ended approach, but there has been a considerable amount of debate about the type of ecosystem that it should aim to restore (Box 1).

Box 1. Benchmarks for Rewilding

Ecosystems that existed during eras before modern humans have been suggested as benchmarks for rewilding. These eras include:

- **The Eemean interglacial** (between ice ages; 132,000 – 113,000 years before present).[19] This came before large animal extinctions linked to the spread of modern humans.[20] In North America and Europe, some propose that the role of now-extinct elephants and lions could be filled by introducing non-native equivalents.[21,22]
- **The early to mid-Holocene** (10,000 - 5000 years before present). Before widespread settled agriculture, landscapes may have been more forested than at present (but still up to 50% open). This followed extinctions of large animals, which may have previously opened up the canopy.[23]

However, restoring land to a historic state is not always possible. Rewilding in human-altered landscapes could lead to the emergence of novel combinations of species,[24] and some proponents suggest that rewilding should take inspiration from the past, but not replicate it.[16]

Rewilding Methods

Reduced management alone can restore natural processes. It may be done deliberately, as in strict forest reserves with little or no human intervention,[25] or unintentionally, as with unprofitable farmland being abandoned across the EU.[26] Another example is the halt in human activities in the Chernobyl exclusion zone following the 1986 disaster. However, in other circumstances human interventions may be needed to restore functioning natural processes.

Kick-starting Natural Processes

Natural processes may be kick-started in several ways; for example, where seed sources no longer exist, trees can be planted and fenced off to assist vegetation succession. This is being done at Carrifran and Glen Affric in Scotland.[27,28] Furthermore, straightened river channels can be "re-meandered" to restore natural flood dynamics upstream [POSTnote 484]. Reintroductions of carnivores and herbivores can also help to restore natural processes,[4] as can removal of invasive species such as rats.[1] However, animal reintroductions are not always feasible and some stakeholders argue rewilding can be done without them.[29]

Carnivore Reintroductions

Thousands of years of large carnivore declines worldwide have had significant ecological effects.[30] For instance, hunting of the Eurasian lynx in Finland and Scandinavia caused numbers of red foxes to increase, which led to declines in numbers of the fox's prey and competitor species.[31] If human pressures diminish then predators at the top of the food chain may recover by default; this happened following Chernobyl with the recovery of wolves.[32] Wolf numbers have also increased across Europe more widely, partly because of protective legislation.[33] Reintroductions can also be used to restore predation; for example, the reintroduction of wolves to Yellowstone National Park controlled the numbers and behaviour of American elk. This allowed vegetation succession in some areas and provided benefits for wildlife more broadly.[34] In the UK, species-level conservation programmes have reintroduced white-tailed eagles to Scotland[35] and boosted pine marten populations in Wales by transferring animals from Scotland.[36]

Herbivore Reintroductions

Some large wild herbivores, such as aurochs and elk, have been extinct or declining for thousands of years.[37] They play a key role in ecosystem function by distributing seeds and nutrients throughout landscapes in their dung.[38] They also play a key role in regulating vegetation succession, for example by grazing grasslands or the leaves of shrubs and trees.[39] As with carnivores, herbivore numbers sometimes recover without human intervention when human pressures subside. For example, densities of European elk are at least as high in the Chernobyl exclusion zone as in nearby nature reserves.[40] Otherwise herbivores can be reintroduced: At the Oostvaardersplassen nature reserve in the Netherlands, introduced heck cattle and konik ponies are intended to fill the role of extinct herbivores such as aurochs and tarpan.[41] In the UK, herbivores have usually been introduced to fenced areas. Many are partially domesticated, although a few elk have been reintroduced at Alladale, Scotland.

Ecological Engineers

Some species are of interest because of how they influence the structure of the environment. For example, beavers cut down trees and build dams that might help prevent flooding (Box 2). Wild boar root around deeply in the soil, disturbing it and preparing it for new vegetation to establish.[42] In the UK, several breeding populations of wild boar have re-established accidentally,[43] and beavers have been reintroduced to rivers in Devon,[44] Knapdale and Tayside.[45]

Benefits and Risks of Rewilding

There are gaps in the evidence base on the consequences of rewilding. This is partly because projects are scarce; the Rewilding Britain NGO lists 13 key projects on its web site.[46] In addition, the impacts of existing projects are difficult to gauge without appropriate control data. However, studies of natural processes shed light on the likely benefits and risks.

Benefits

Reduced Management Costs

The cost of land management is substantial, whether for agriculture, wildlife or other ecosystem services. Over half of total farming income in the UK derives from EU subsidies,[47] and many farms might not be economically viable without them.[48] In addition, public spending on conservation in Sites of Special Scientific Interest (SSSI) is around £85 per hectare per year, including payments to landowners for environmental management.[49] Rewilding approaches can provide biodiversity gains and reduce the need for human management. For example, blocking drains can restore wetland habitats without much further input from people.[50] Reintroduced animals can have the same effects on habitats as management measures formerly carried out by people; for instance, wolves can control numbers and behaviour of deer and reduce the need for culling.[51]

Biodiversity and Recreation

A reduction in human management can lead to an increase in biodiversity. For example, abandoned crop fields at the Rothamsted Experimental Station in Hertfordshire developed into diverse mature woodlands within a century.[52] At the Knepp Wildland Project, many species benefit from a mosaic of habitats produced through grazing by de-domesticated breeds of herbivores (Box 3). This provides opportunities for recreation; global demand for nature tourism is so high that visits to protected areas generate

Box 2. Beavers as Ecological Engineers in Devon

Beavers create leaky dams in rivers and streams. These cause localised flooding, creating complex wetland habitats that increase beavers' food supply and protect their burrows from predators.[53] After rainfall, beaver dams trap sediment and reduce peak flow downstream (Figure 1).[54] They also filter agricultural pollutants such as nitrates and phosphates.[55] However, burrowing, tree felling and localised flooding create costs for local land managers. A beaver management strategy has been produced for the River Otter to help mitigate these impacts, with relocation and lethal control proposed as a last resort.[56]

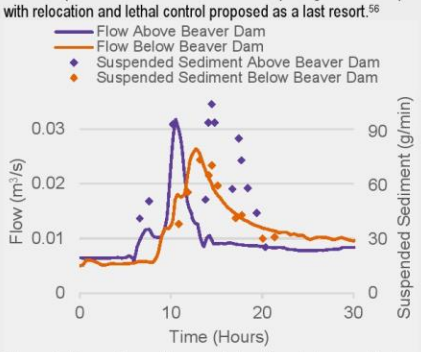

Figure 1. Stream flow and suspended sediment above and below a beaver dam following rainfall at the Devon Beaver Project. Peak flow is lower below the dam and delayed by several hours. Sediment levels are also reduced below the dam, meaning that water was cleaner.[55]

$600bn in revenue each year.[57] Rewilding has the potential to increase revenue from tourism, attracting people firstly as a label that is rapidly increasing in popularity,[15] and secondly through opportunities to see charismatic species. For example, White-tailed eagles have become a wildlife spectacle in Scotland, generating up to £5m a year in tourist spending on the Isle of Mull.[58,59] Ospreys are also a significant tourist attraction on Rutland water in England.

Flood Prevention and Water Quality

Rewilding may have benefits for flood prevention and water quality,[6] examples include:

- Wetland restoration. This can incorporate rewilding approaches; it involves blocking man-made drainage systems and letting habitats develop naturally.[50] Wetland habitats such as blanket bog retain water and decrease water treatment costs,[60] so water companies like United Utilities and South West Water invest in restoring them. Wetland restoration is also happening at large scales, such as the Great Fen Project in Cambridgeshire.[61] However, these habitats may also increase prevalence of bog asphodel, a plant that can poison sheep that eat it.[6]
- River restoration. Re-meandering rivers can reduce flood risk on land downstream; this is done at the Eddleston water project in Scotland.[62] The river Liza at Wild Ennerdale in the Lake District is allowed to shift freely in response to heavy rainfall, so it drops lots of sediment before reaching Ennerdale lake.[63]
- Vegetation succession. The Wild Ennerdale initiative has reduced sheep grazing and seeks to increase tree cover through regeneration of native woodland. These factors can result in greater absorption and reduced runoff of water from land, reducing flood risk downstream.[64]
- Beavers. Dams built by beavers can reduce peak flows downstream and improve water quality (Box 2).

Box 3. Rewilding at the Knepp Wildland Project

Knepp Castle Estate in Sussex comprises 1,400ha of heavy clay soils, so landowners have struggled to make a profit through arable and dairy farming. Since 2001, all available land has been taken out production and put into a rewilding project.[65] It aims to restore natural ecological processes using free roaming herds of grazing and browsing animals as drivers.[39] This involved removing internal fences and giving deer and hardy breeds of pigs, cattle and ponies free roam of the estate. The emerging scrub, wood-pasture, water meadows and grassland currently support some of the largest UK populations of Nightingales, Turtle Doves and Purple Emperor Butterflies. The estate has reduced its agricultural input costs, and receives income from organic meat sales and Common Agricultural Policy payments. Furthermore, a new camping and ecotourism enterprise employs three people full time; it had a turnover of £120,000 in the first year, with a profit of £19,000 that looks set to increase in future. Farm turnover under conventional farming was £1.2m with a return on capital of -2% to +1%, whereas today turnover is £1m with return on capital of 5%.

Greenhouse-Gas Emissions

There are potential benefits of rewilding for GHG emissions. Agriculture contributes 9% of the UK's greenhouse-gas (GHG) emissions, such as nitrous oxide, methane and carbon dioxide and 10-12% globally [POSTnotes 453 & 486]. Reducing intensive management of farmland through rewilding would be likely to reduce local GHG emissions.[66] Habitats resulting from rewilding may also have the potential for storage of carbon and nitrogen [POSTnote 447]. For example, woodlands that developed on former crop fields at Rothamsted store an additional two tonnes of carbon and 20kg of nitrogen per hectare per year, although the amount gained varied between sites.[67] Restored wetlands are carbon dioxide sinks, but they are also a source of methane [POSTnote 454].[68] A recent UK study found that increasing agricultural yields on reduced areas of farmland while restoring habitat on 'spared' land could reduce GHG emissions and keep food prices low.[69]

Risks

Unpredictable Outcomes

Rewilding is likely to lead to an increase in biodiversity, but outcomes are often unpredictable and unique to each site. Many species will benefit from rewilding, but others may decline – especially those that depend on features currently maintained by human intervention. Around 1-in-5 UK butterfly species (18%) inhabit open habitats that result from traditional agricultural practices[70] and rewilding could lead to different types of habitat.[71] Increasing the scale and interconnectedness of habitats through rewilding may help some species adapt to climate change, but others might fare better where humans continue to intervene.[72,73] Furthermore, animal reintroductions can have unpredictable outcomes. The IUCN (the world conservation union) have produced guidelines emphasising the need for comprehensive risk assessments and warning against releasing species outside their indigenous range.[74] An evidence-based framework is needed to select species suitable for reintroduction in any given case.[4]

Attitudes to Reintroductions

Stable or rising populations of lynx, wolves and bears in Europe show that human-predator coexistence is possible.[33]

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However, range expansions and reintroductions of animals tend to cause conflict between groups of people with different values.[75] For example, some people enjoy seeing wild boar in UK woodland, but others call for culls to prevent crop damage.[43] White-tailed eagles are appreciated by tourists and conservationists in Ireland and Scotland, but they take some sheep farmers' lambs (although some argue that livestock losses are economically negligible).[58,76] Conflicts can sometimes be avoided by creating consensus management plans for the reintroduction of a species.[77,78]

Animal Control and Welfare

In the absence of wild predators, ongoing human intervention might be required to control numbers of some animals. Managers at the rewilded Oostvaardersplassen nature reserve faced conflict from animal welfare campaigners over winter mortality of cattle and ponies prevented from moving out of the reserve.[79] The notion that these animals were "wild" was contested, implying they should not be exempt from animal welfare regulations. Reserve managers were granted exception from animal welfare, but they reached a compromise in which they shot animals deemed unlikely to survive the winter. This compromise continues to face international criticism.[80]

Making Space for Rewilding

Rewilding needs to be reconciled with other forms of land use that benefit people, such as agriculture. Some argue that rewilding of less productive farmland could more than compensate for biodiversity losses on intensively managed crop fields [POSTnote 418]. Compared to Bulgaria, Estonia, Latvia, Poland, Romania, Slovenia and Slovakia the UK has a very limited area that could be described as wilderness,[81] and rewilding could improve this.[82] Some point to upland areas, where farmers are highly dependent on income support,[83] as candidates for rewilding.[17] However, in the case of the Wild Ennerdale project, some upland farmers criticised the changed appearance of the landscape and voiced concerns about the loss of the farming heritage of the region.[84] The Scottish Highlands is thought to be the main UK region that could support populations of large predators,[85] with enough woodland and prey to potentially support 400 lynx.[86] However, at smaller scales, the Rewilding Britain NGO argues that even post-industrial sites in urban areas can be rewilded. They recommend that local communities have ownership of the rewilding process.[46]

Rewilding and UK Policy

No UK government policy or statement refers to rewilding explicitly. However, rewilding is relevant to many policy areas including agriculture, natural capital and biodiversity.

Agricultural Policy

The UK must adhere to the Common Agricultural Policy (CAP) while it remains a member of the EU, and the same level of agricultural support will continue until 2020 regardless of exit from the EU. The CAP forms 40% of EU spending,[87] and constrains rewilding in three main ways:

- 70% of CAP payments to farmers are conditional on land in "good agricultural condition". Land must be suitable for grazing or cultivation, and free from "ineligible features", such as dense scrub that may arise through rewilding.[88]
- Some CAP payments require livestock grazing. Projects are inclined to use livestock to receive payments, but this may not be the best way of restoring natural processes.[82]
- CAP payments raise the market value of marginal farmland; acquiring such land for rewilding is expensive.[89]

Though a small proportion of CAP funding is spent on environmental protection, some have argued that the CAP fails on biodiversity and non-food ecosystem services.[90] Policymakers have also suggested that post Brexit landowners could be paid for providing specific ecosystem services, such as flood prevention.[91] Rewilding measures might be applicable to this end. Up to now, rewilding projects such as the Alladale wilderness reserve in Scotland[92] have been funded by landowners with alternative views on land use. Other projects are supported by crowd-funding; Trees for Life volunteers have paid for and planted over a million trees for rewilding in the Scottish Highlands.[28]

Natural Capital

Natural capital has been defined as "the parts of the natural environment that produce value to people", such as clean air and water, food, and protection from hazards.[93] Preliminary accounts suggest that the UK's natural capital is declining,[94] and the Government's plan for the natural environment will set targets to address this. The Rewilding Europe NGO suggests that as a complement to existing conservation practices, rewilding can help to create new natural assets.[16] However, this will depend on how benefits from rewilding trade-off with benefits from other land-uses.[83]

Biodiversity Policy

Rewilding may represent a cost-effective way to restore large areas of degraded habitat and reintroduce native species. However, because of unpredictable outcomes rewilding may not deliver other UK commitments on biodiversity (Box 4). Additionally, some UK legislation may form a barrier to reintroductions. For example, it is illegal to release wild boar in England and Wales.[95] Ongoing management is likely to be required to meet commitments on weeds or non-native invasive species; even strict forest reserves are managed by people to control rhododendron.[25]

Box 4. Biodiversity Policy in the UK

Legislative commitments on biodiversity are derived largely from the international conventions including the Bern convention on the Conservation of European Wildlife and Natural Habitats[96] and the Bonn convention on the Conservation of Migratory Species of Wild Animals.[97] Key legislation includes the Wildlife and Countryside Act,[95] Nature Conservation (Scotland) Act,[98] the Wildlife and Natural Environment Act (Northern-Ireland),[99] the Environment (Wales) Act[100] and the EU Nature Directives.[101,102] Legislation:

- Protects priority animals (including most birds), plants and habitats.
- Provides for the SSSI/ASSI (Site/Area of Special Scientific Interest) and Natura 2000 protected area networks to maintain habitats.
- Pledges reintroduction of native species of wild plants and animals if studies show it is effective and acceptable.

The Convention on Biological Diversity[103] outlines further pledges to restore degraded habitats, and has stimulated the "Biodiversity 2020" strategies for England,[104] Northern Ireland[105] and Scotland.[106]

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Appendix P2: Habitat creation through the Common Agricultural Policy benefits insect populations - Submission to the Environmental Audit Committee

I prepared this document for the Environmental Audit Committee in response to their inquiry regarding "The Future of the Natural Environment after the EU Referendum". It represents my presonal attempt to (1) raise the committee's awareness about the reasons to conserve insect biodiversity on farmland and (2) present key evidence emerging from my PhD project as well as other studies of EU-funded AES interventions.

Habitat creation through the Common Agricultural Policy benefits insect populations

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Most species of insects are not pests; rather, many play economically valuable roles as pest control agents, pollinators of wildflowers and crops, food for birds and fish, and sources of fascination and inspiration for people.[1] Furthermore, the few insect groups that have been adequately monitored show declining trends linked to agricultural intensification.[2] Direct payments to farmers through the Common Agricultural Policy (CAP) can encourage intensive farming, but 6% of the CAP budget funds agri-environment schemes (AESs) that can benefit wildlife.[3] In this submission I summarise evidence that CAP-funded AESs benefit insect populations,[*] and make suggestions to optimise delivery of future agri-environmental policy in the UK.

CAP-funded habitat creation increases the variety and abundance of insects

My colleagues and I have focussed on the impact of AES-funded habitat creation on the abundance and species-richness of moths. Moths are the major nocturnal pollinators[4] and like many other insect groups they have been in decline due to agricultural intensification.[5] In 2014, I used light traps to measure the abundance of moths on 32 crop field margins in southern England, half of which had AES-created grassland strips on them. I found slight positive effects of grassland strips on the abundance of all types of moths, but the effect was particularly strong for grassland moths (Figure 1) which were ~1.5 times more abundant on grassland strips.[6] Grassland strips provide nectar for adult moths, but also a variety of plant species for their caterpillars to eat. They are also less exposed to pesticides known to kill moths.

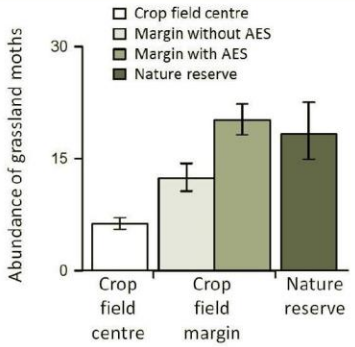

Figure 1. Average abundance of grassland moths (±95% confidence intervals) on the centre of a crop field (left), on crop field margins with/without AES-created grassland strips (centre left/centre right) and on chalk grassland nature reserves (right).

Benefits of AES-created grassland strips have also been shown for UK bumble-bee species, especially when strips are sown with nectar-rich flowers.[7] Furthermore, evidence from the Swiss AES shows that increasing the abundance of pollinating insects in this way can increase the seed-set of agricultural plants.[8] Another UK study concludes that creating grassland strips doesn't necessarily decrease crop yield at the field scale.[9]

AES habitat creation also occurs at scales larger than just the field margin. In 2015 I measured moth abundance on 64 crop fields, half of which had been entirely converted to species-rich grassland and were maintained under AESs. Grassland moths were ~3.5 times more abundant on created grasslands, while moths considered to be specialised to chalk grassland were almost 8 times more abundant on created grasslands.[10] Previous research has shown that the variety of plant species on created grasslands takes more than 60 years to strongly resemble that on ancient grasslands,[11] but our work suggests that large-scale habitat creation can still lead to remarkable increases in the variety and abundance of insects.

[*] "Agri-environment scheme" is a catch-all term for the subsidy of a wide range of practices – reducing fertilizer inputs on grasslands, growing trees in hedgerows, taking up organic farming, etc. I present evidence about the effects of habitat creation funded by AESs. I define this as converting areas of intensively farmed land (such as crop monocultures) to extensively managed habitats like species-rich grasslands.

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How can future policies maximise the benefits of habitat creation for insects?

Not all forms of AES have been shown to benefit insects, and studies across Europe suggest that benefits are biased towards common species.[12] This is not necessarily a problem; a small number of common species of wild bees make a huge contribution to crop pollination across Europe.[13] However, this does highlight a conflict whereby optimising the outcomes of agri-environmental policy will depend on the relative value ascribed to (1) conserving species that are threatened, and (2) conserving species for services they provide. Even so, the following might be used to maximise the outcomes of AES habitat creation for insects:

Spatial targeting of AES habitat creation: During field work in 2014 I found evidence that moth species specialised to chalk grassland could only benefit from grassland strips created within ~1km of some long-standing chalk grassland.[6] Evidence collated across Europe suggests that AESs tend to have more benefits for wildlife in landscapes with intermediate amounts of long-standing habitat, rather than in landscapes which already have over 20% coverage of habitat.[14]

Management to introduce wildflower species to created habitats: Hay from existing species-rich grasslands can be applied to created grasslands to introduce a variety of rare plants.[15] In 2015 I found that increasing the variety and frequency of these plants leads to an increase in the abundance of associated moths.[10] This effect holds true for a wide range of insect groups.

Accepting occasional trees and shrubs on created habitats: Hedgerows at field margins provide shelter and resources for many insect groups, especially moths (Figure 1). Furthermore, my work shows that chalk grassland nature reserves are benchmark sites for wildlife, partly because they contain woody vegetation. Evidence is accruing that negative effects of shrub and tree growth on species have been overstated;[3] future policies might encourage these features on created habitats to increase the abundance of insects and the benefits they provide to people.

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Summary

- Insects are valuable pollinators, pest control agents, and food sources for wild animals.
- CAP-funded habitat creation, such as converting crop fields into species-rich grasslands, has led to significant increases in the variety and abundance of insect species.
- For some insects, AES-created habitats can be more beneficial if close to existing habitat.
- Establishing rare wildflowers on created habitats can benefit associated insects.
- Encouraging occasional trees and shrubs can provide more resources for insect species.

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